Cladistics and the Biogeography of Two Trans-Caribbean Hairstreak Butterfly Genera: *Nesiostrymon* and *Terra* (Lepidoptera, Lycaenidae)

KURT JOHNSON[1]

ABSTRACT

Two sister genera composed of notably non-vagile members distributed both in the Greater Antilles and mainland Neotropics are revised. Cladistic classification is employed from numerical analysis (PAUP, Swofford) of the ingroup and three outgroups restricted to the mainland. *Nesiostrymon* includes five species: in the Antilles, type species *N. celida* (Lucas) (with three interisland subspecies—nominate [Cuba] *N. c. aibonito* (Comstock and Huntington) [Puerto Rico and northern Hispaniola], *N. c. baorucoensis,* new subspecies [southern Hispaniola]), and *N. shoumatoffi* (Comstock and Huntington) (Jamaica); on the mainland, pan-Neotropical *N. celona* (Hewitson) (transferred from *Thecla*) and two new insular species, *N. milleri* (cloud forests, Aragua, Venezuela) and *N. australivaga* (scrub-steppe, Mendoza, Argentina). *Terra* includes six species: in the Antilles,

T. hispaniola Johnson and Matusik (southern Hispaniola); on the mainland, type species *T. tera* (Hewitson) (central Mexico to Colombia); three species transferred from *Thecla, T. calchinia* (Hewitson) (upper Amazon), *T. cana* (Hayward) (northwest Argentina), *T. chilica* (Schaus) (southeast Brazil, Paraguay); and one new species, *T. andevaga* (Ecuador). Comparison of area cladograms of *Nesiostrymon* and *Terra* shows congruence of plesiotypic Antillean elements and apotypic members occurring in Central America and South America, respectively. These are construed as more compatible with late-Cretaceous-Tertiary vicariance of a proto-Greater Antilles from the Central and South American regions than a complex dispersal explanation requiring numerous concordant dispersals.

[1] Research Associate, Department of Entomology, American Museum of Natural History.

INTRODUCTION

Nesiostrymon Clench (1964) and *Terra* Johnson and Matusik (1988) are sister genera of notably nonvagile "hairstreak butterflies" (Theclinae, Eumaeini) occurring both in the Antilles and the mainland Neotropics. Numerical cladistic analyses associated with the description of *Terra* indicated that it and *Nesiostrymon* are the sister group of three eumaeine assemblages restricted to the mainland (Johnson and Matusik, 1988). Observing the local habitat restriction and widely disjunct distributions of *Nesiostrymon* and *Terra* taxa, Johnson and Matusik (1988) suggested that Antillean species of these genera (along with two other recently discovered south Hispaniolan endemics) most likely "reflect a tectonic relationship between . . . regions . . . on the northern edge of the Caribbean plate."

Recent biogeographical studies (Shields and Dvorak, 1979; Buskirk, 1985; Johnson and Descimon, 1989; Miller and Miller, 1989) recognized a component of Antillean Rhopalocera more suggestive of an ancient vicariant origin than the prominent waif-dispersal origin attributed to the fauna by early workers (Comstock and Huntington, 1949; Scott, 1972; Riley, 1975; Brown, 1978). Miller and Miller (1989), summarizing a probable vicariance and dispersal model for Antillean butterfly origins, included *Nesiostrymon* and *Terra* as one of nine butterfly groups most probably arising from late Cretaceous-Eocene vicariance.

This study reports a cladistic taxonomy of Neotropical *Nesiostrymon* and *Terra* and presents the ecological and biogeographic evidence supporting a vicariant origin for Antillean members of these two hairstreak butterfly genera.

MATERIALS AND METHODS

COLLECTIONS

Specimens examined included samples from the Allyn Museum of Entomology, Florida Museum of Natural History (AME); American Museum of Natural History (AMNH); British Museum (Natural History) (BMNH); Carnegie Museum of Natural History (CMNH); Field Museum of Natural History (FMNH); Hope Entomological Collection, Oxford University (HEC); Instituto Miquel Lillo (Tucumán, Argentina) (IML); Los Angeles County Museum (LACM); Milwaukee Public Museum (MPM); Museum National d'Histoire Naturelle (Paris, France) (MNHN); Museo Nacional de Historia Natural (Santo Domingo, Dominican Republic) (MNDR); Zoologisches Museum der Humboldt Universität zu Berlin (ZMH). Specimens were also examined from three private collections with extensive Antillean or austral South American holdings: Robert C. Eisele Collection (Jujuy, Argentina) (REC); David Matusik Collection (Skokie, Illinois) (DM); and Albert Schwartz Collection (Miami, Florida) (ASC).

SYSTEMATICS

Phylogenetic Analyses of *Nesiostrymon* and *Terra*: Johnson and Matusik (1988) used numerical cladistic analysis (PAUP; Swofford, 1985) to establish the monophyly of *Nesiostrymon, Terra,* and certain outgroup taxa of the lycaenid grade "*Thecla*" (sensu Bridges, 1988) (fig. 1; tables 1, 2). Focusing primarily on the Caribbean region, Johnson and Matusik (1988) distinguished Antillean members of *Nesiostrymon* and *Terra* and listed mainland relatives from the "*Thecla*" grade. Subsequently, Johnson (1991) published a nomenclature for outgroup taxa (figs. 84, 85).

The cladistic study of Johnson and Matusik (1988) indicated that *Terra* and *Nesiostrymon* form a monophyletic group distinguished from outgroups by six synapomorphies of the wings, genitalia, and terminal abdominal morphology (table 1: characters 2, 4–6, 12, and 14). *Terra* taxa share a salient apomorphy: the prominent sclerotized bulb protruding ventrally between the cephalic and caudal elements of the ductus bursae (table 1, character 11). *Nesiostrymon* taxa share a specialized prominently pronged tergite 8 in males (table 1, characters 1, 9). High consistency values (fig. 1) for cladograms result from the various very distinctive morphological characters which separate these taxa (e.g., the incised posterior cavity of male tergite 8, distribution of microtrichia, etc.). "Outgroup" and "Lundberg outstate"
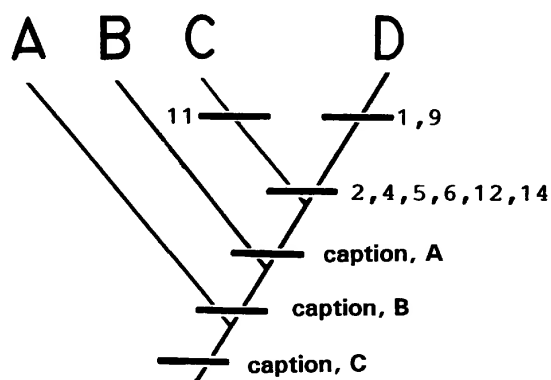
Fig. 1. Cladogram of *Nesiostrymon* (D), *Terra* (C), and relatives (A, B) (Johnson and Matusik, 1988). Four-taxon statement derived from parsimonious distribution of unweighted characters and rooted using (1) outgroup[s] described in text (consistency index = 0.923) and (2) Lundberg method (Swofford, 1985) based on presumed primitive states listed at bottom of table 2 (consistency index = 0.889). Apomorphies for *Nesiostrymon* and *Terra* specified by horizontal bars enumerated from tables 1 and 2. Outgroups and their apomorphies: A, B. Outgroup rooting preferred "*Thecla uzza* complex" (fig. 84) as sister group of *Nesiostrymon/Terra* based on characters 9, 10 with "*Thecla celmus* complex" (fig. 84) as the outgroup; Lundberg rooting preferred the opposite based on characters, 1, 3, 7, 13. C. "*Thecla*" outgroup (fig. 85), characters enumerated by Johnson and Matusik, 1988.
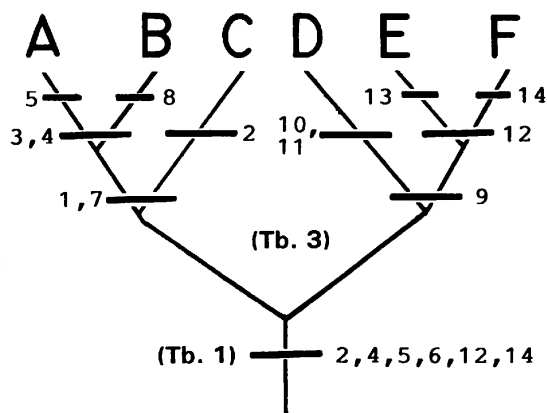

Fig. 2. Ingroup cladogram of *Nesiostrymon* (A, B, C) and *Terra* (D, E, F). Six-taxon statement derived from parsimonious distribution of unweighted characters and rooted using Lundberg outstates based on monophyly of *Nesiostrymon* and *Terra*, figure 1. Consistency index = 0.909. Apomorphies are specified by horizontal bars and represent characters enumerated in tables 3 and 4. Synapomorphies noted for *Nesiostrymon/Terra* are from figure 1, tables 1 and 2. Terminal groups include A, *N. celona/milleri/australivaga*; B, *N. celida*; C, *N. shoumatoffi*; D, *T. hispaniola*; E, *T. tera*; F, *T. andevaga/chilica/calchinia/cana*.

(Swofford, 1985) rootings (fig. 1) give identical results concerning the monophyly of *Terra* and *Nesiostrymon*.

To determine a cladistic classification of species in *Nesiostrymon* and *Terra*, parsimonious distributions of characters were constructed for shared characters of species in each genus (fig. 2, tables 3, 4). Monophyly of the ingroup was assumed from Johnson and Matusik's (1988) results; species criteria were based on standard taxonomic procedures involving consistent differences in characters of the wings and genitalic and tergal morphology. Table 3 lists the apomorphic and plesiomorphic states of characters delimited from the final rooted tree (fig. 2). This analysis indicates the following: *Nesiostrymon* is a monophyletic group with two nested sets of taxa, the Jamaican endemic, *N. shoumatoffi*, being the most primitive in character; *Terra* is a monophyletic group with two nested sets of taxa, southern Hispaniolan endemic *T. hispaniola* being the most primitive in character. Based on these results, species-level taxonomies for *Nesiostrymon* and *Terra* are enumerated below.

TAXONOMY OF *NESIOSTRYMON* and *TERRA*

GENUS *NESIOSTRYMON* CLENCH
Figures 3–32, 57, 59–68

Nesiostrymon Clench, 1964: 248, 251. Brown and Heineman, 1971: 4; 1972: 232. — Scott, 1986: 21. — Riley, 1975: 101. — Bridges, 1988: I.74, II.77. — Johnson and Matusik, 1988: 236. — Schwartz, 1989: 240. — Miller and Miller, 1989: 245.

DIAGNOSIS: Compared to all Eumaeini: male tergite 8 modified to a "subcordate incised posterior cavity" (the "*sipc*" sensu Field, 1967a, 1967b; Johnson, 1988a, 1989a, 1989b; Johnson and Matusik, 1988) terminating in a dorsally produced lobe or prong, genital valvae multiplanar with protruding, winglike lateral lobes; female genital ductus bursae exhibiting heavily sclerotized, opaque caudal

and cephalic elements separated by a transparent neck; both sexes' wing under surfaces gray-white, crossed by a jagged or disjunct black medial band. Compared to *Terra*: *Terra* male tergite 8 unmodified and genital valvae flat and uniplanar; female ductus bursae with bulblike sclerotized element protruding basally from transparent ductal neck; wing under surfaces with medial yellow, orange, or reddish bands.

DESCRIPTION: *Adult.* Body fuscous, finely overlaid with gray to bluish hairlike scales and setae; eyes ringed with white; antennae black, finely striped with white. *Male.* Upper Surface of Wings: apical and marginal areas of wings fuscous to black; rest of wings brilliant iridescent blue. Large elliptic androconial element (hereafter, the "brand" sensu Eliot, 1973) in distal area of discal cell variously overlapping blue ground color. Hindwing with long tail at terminus of vein CuA2, short tail at terminus of vein CuA1. Under Surface of Wings: ground color white to gray with jagged to disjunct medial and/or submarginal bands formed by black dots or slashes in the wing cells (most commonly a disjunct black medial band on each wing). Limbal area with prominent eyespot at margin of cell CuA1 (the "Thecla spot" sensu Clench, 1961). Length of forewing: 8.0–12.5 mm. *Female.* Upper Surface of Wings: similar to those of male but structural color duller, fuscous margins and apices wider, forewings without brands. Under Surface of Wings: Similar to those of males. Length of Forewing: 9.0–13.0 mm. *Male Tergal Morphology and Genitalia* (figs. 57, 60, 61, 63, 65, 66, 68). *Sipc* terminating in dorsal lobe or prong of varying length. Dorsoterminal surface of genitalia with two small "brush organs" (sensu Eliot, 1973) abutting lateral edge of vinculum; length of brushes not exceeding terminus of labides. Genitalia with lateral surface of vinculum tapered smoothly between labides and saccus (not angled as in *Terra*); saccus greatly elongate, cephalically distending the vinculum; valvae, compared to other Eumaeini, very small, length of caudal extensions not exceeding ventrocaudal length of vincular arc (fig. 57) and shaped distinctly multiplanar with winglike lateral lobes protruding at different lengths in the various species; valval terminus, where most

eumaeines have an extended caudal lobe, with only a disjunct, slightly sclerotized pad (the "extravalvular element" sensu Johnson and Matusik, 1988); aedeagus elongate (length usually exceeding rest of genitalia by at least one-third) with caecum short (comprising one-fifth to one-seventh of aedeagus length, depending on the species) and terminus undulate; terminus of aedeagus with two spinelike cornuti. *Female Tergal Morphology and Genitalia* (figs. 59, 62, 64, 67). Tergite 8 unspecialized but papillae anales modified by heavy sclerotization to a steeply pointed, nearly opaque terminus; ductus bursae divided into darkly sclerotized caudal and cephalic elements separated by a transparent neck, relative length and shape of respective caudal and cephalic elements varying greatly between the species; ventral opening of ductus terminus with thin transverse lamellal lips; juncture of ductus bursae to corpus bursae blunt, without distinctive structural elements at the cervix bursae; signa broadly based sclerotized plates with a raised, cephalically directed keel.

TYPE SPECIES: *Thecla celida* Lucas (1857) by original designation. Clench (1964) designated *N. celida* as type, illustrating what he considered the Jamaican "subspecies" (*shoumatoffi* Comstock and Huntington). Although the latter is clearly a distinct species, I consider *T. celida* the type, consistent with Clench's taxonomy.

DISTRIBUTION (fig. 81): Central Mexico southward to central Argentina; in the Antilles (Cuba, Puerto Rico, Hispaniola, Jamaica).

DISCUSSION: Contrary to Clench's original view (1964), *Nesiostrymon* is not an endemic Antillean genus (see Biogeography). Rather, it includes two Antillean species (one with three distinctive allopatric populations) and three species on the mainland (two of which are undescribed). Referring to the present revisionary study, Johnson and Matusik (1988) informally listed *Thecla* species possibly belonging in *Nesiostrymon* and Bridges (1988) followed this list in his index of *Thecla* taxa. Accordingly, and since Bridges (1988) did not use formal binomials in his index, I consider the present work as establishing the new combinations and synonymies cited in the taxonomy below.

TABLE 1
Characters of *Nesiostrymon*, *Terra*, and Relatives Used for Figure 1 Cladogram Construction

(apomorphic (A) and plesiomorphic (P) states for characters of table 2 matrix; descriptions and terminology as noted below[a])

Tergal Morphology

1. Male, condition of tergite 8: (A) tergite 8 heavily sclerotized throughout, forming incised posterior cavity of subcordate shape (the "*sipc*" sensu Field, 1967a, 1967b; Johnson, 1988a, 1989a, 1989b) (figs. 57c, d, 60, 61, 63, 65, 66, 68); (P) tergite 8 normal (sensu Johnson, 1989a) (figs. 58c, d, 69, 72, 73, 74, 78–80).

Genitalia

2. Male, configuration of saccus: (A) length of saccus equal to or exceeding 2.5 times "radius of vincular arc" (fig. 57a, b); (P) ventrum of vinculum generally entire or with saccus development negligible (saccus length equal to or less than radius of vincular arc) (figs. 84a, b, d–g; 85a–c, e).

3. Male, configuration of vinculum: (A) "caudoventral diameter of vincular arc" (fig. 57a) equal to (or within 0.2 standard deviation from saccus length (fig. 85c); (P) caudoventral diameter of vincular arc equal to at least twice saccus length (fig. 84a, d–g; 85a–c, e).

4. Male, configuration of vinculum: (A) radius of vincular arc less than length of saccus (figs. 57, 58); (P) radius of vincular arc equal to or greater than length of saccus (figs. 84a, b, d–g; 85a–c, e).

5. Male, valvae "caudal extension" (figs. 57a–58a): (A) length of valves not exceeding caudoventral diameter of vincular arc (figs. 57–58, 61, 63, 65, 66, 68, 72, 73, 74, 78–80); (P) valvae caudal extensions tapered to various lengths exceeding caudoventral diameter of vincular arc (figs. 84a, e–g; 85a–c).

6. Male, condition of valval apparatus at caudoventral extreme of vincular arc (figs. 57–58): (A) area caudad of valvae apex and basal to arch of falces with a membrane-enfolded, ellipsoidal sclerotized pad (the "extravalvular element" sensu Johnson and Matusik, 1988, figs. 57a–58a); (P) see entry 5, P (figs. 84a–g; 85a–c).

7. Male, aedaegus: (A) length (measured along lateral surface, including length of caecum displaced outside the plane of aedeagal shaft) equal to or exceeding 2.75 times the caudoventral diameter of vincular arc (figs. 57aa–58aa); (P) length (measured as above) variously less than 2.75 times the caudoventral diameter of vincular arc (measured as above) (taxa of fig. 84a, d–g; 85a–c [aedeagus not figured]).

8. Female, configuration of ductus bursae: (A) ductus bursae divided into respective caudal and cephalic elements connected by a "transparent neck" (figs. 59, 62, 64, 67, 69, 70, 71, 75–77); (P) ductus bursae of contiguously opaque sclerotization (figs. 84b–h; 85a–c, e).

9. Female, condition of transparent neck: (A) transparent neck smooth (uninterrupted by sculpturing or additional components) over entire circumference (the "simple" condition characterized by Johnson and Matusik, 1988) (figs. 59, 62, 64, 67); (P) see entry 8, P (figs. 84b–h; 85a–c, e).

TABLE 1—(*Continued*)

10. Female, condition adjacent transparent neck: (A) transparent neck with prominent ventrally directed ovate sclerotized element (the "bulb" [fig. 69] sensu Johnson and Matusik, 1988) (figs. 69, 70, 71, 75–77); (P) see entry 9, A (figs. 59, 62, 64, 67).

11. Female, condition of bulb (fig. 69): (A) bulb located about equidistant from caudal and cephalic ductal termini (fig. 69, 70, 71, 75–77); (P) bulb occurring at cephalic base of ductus bursae, abutting distal end of corpus bursae (see Johnson and Matusik, 1988: 241) (fig. 84b).

12. Female, configuration of papillae anales: (A) papillae anales with heavy, caudally inclined, lateral sclerotizations forming a pointed terminus (figs. 59, 62, 64, 67, 69, 70, 75, 77); (P) papillae anales lobate, with evenly distributed sclerotized elements (taxa of figs. 84; 85a–c [papillae anales not figured]).

Wing Pattern

13. Both sexes, pattern of under surface (figs. 3–56): (A) under surface of hindwing with pattern elements occurring (a) medially at least in cells SC + R1, Rs, M1, M2, M3, CuA1, CuA2, and 2A, and (b) postbasally at SC + R1; (P) pattern more elaborate than above including (a) distally expansive, continuous or lunular median bands, (b) extensive markings in the postbasal area, and (c) pronounced limbal markings in addition to the usual Thecla spot and accordant ground color suffusions (see Johnson and Matusik, 1988: 241).

14. Both sexes, pattern of under surface: (A) under surface of hindwing with pattern elements crossing inside discal cell, and occurring either (a) postbasally in at least one of the following cells: cell SC + R1, cell CuA2, cell 2A; or (b) basally in the discal cell; (P) see entry 13, A.

External Secondary Sexual Characteristics

15. Male, dorsal forewing androconial structures: (A) forewing dorsum of male with ellipsoidal androconial brand (sensu Eliot, 1973) encompassing distal end of discal cell and basal portion of cells M3, M2, M1, and the radial veins (figs. 3, 7, 11, 13, 17, 21, 25, 27, 29, 33, 37, 41, 45, 49, 53); (P) androconial scales lacking or, in a few outgroups cases, concentrated in a small androconial mark limited to the area basad the crossvein of the forewing discal cell (see Johnson and Matusik, 1988: 240).

[a] For consistency, descriptions of apomorphic states follow Johnson and Matusik (1988); terminology follows Johnson and Matusik (1988) and Johnson (1989a, 1989b, 1989c; 1991) with first usage of any term marked with quotation marks.

Studies of Antillean Lepidoptera have traditionally used subspecies categories for distinctive interisland populations. Some of these subspecies complexes exhibit general geographic patterns (Comstock and Hunting-

TABLE 2
Character State Matrix for *Nesiostrymon*, *Terra*, and Relatives
(columns 1–15, characters enumerated in table 1; rows as enumerated below[a,b])

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
A	1	0	1	1	1	1	1	1	1	0	0	1	1	1	1
B	0	0	1	1	1	1	1	1	0	1	1	1	1	1	1
C	0	1	1	0	0	0	1	1	0	1	0	0	1	0	1
D	0	1	1	0	0	0	1	0	0	0	0	0	1	0	1
E	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

[a] Taxa A–E. (A) *Nesiostrymon*, (B) *Terra*, (C) *uzza* complex (enumerated in Systematics and fig. 84), (D) *celmus* complex (enumerated in Systematics and fig. 84), (E) outgroup (enumerated in Systematics and fig. 85).

[b] L. Characters used for Lundberg rooting of parsimonious network.

ton, 1943; Riley, 1975; Scott, 1972; Johnson and Descimon, 1989; Miller and Miller, 1989). Subspecies usage in *Nesiostrymon* is compatible with cladistic results since Antillean *Nesiostrymon* exhibits two nested sets of taxa. Consistent with an equal rank criterion, each nested set corresponds to a species, one with three allopatric island populations having three subspecies. On the mainland, there appears to be no utility in using infraspecific categories (Johnson, 1989c). Below, species of *Nesiostrymon* are organized according to the regional nested sets apparent in the ingroup cladistic analysis (fig. 2, table 2).

ANTILLEAN TAXA

Nesiostrymon celida (Hewitson)
Figures 3–20, 57, 59–61

Thecla celida Lucas, 1857: 610. — Kirby, 1871: 393. — Hewitson, 1869: 125, pl. 49, figs. 246, 247. — Draudt, 1919: 803, pl. 159. — Kaye, 1931: 535, pl. 39, fig. 10 (referring only to *shoumatoffi* Comstock and Huntington, see next entry). — Wolcott, 1936: 402. — Comstock and Huntington, 1943: 76; 1958–1964 [1959]: 181.
Strymon celida: Bates, 1935: 194.
Nesiostrymon celida: Clench, 1964: 248, 251. — Lewis, 1974: 67. — Brown and Heineman, 1972: 232. — Scott, 1986: 21. — Riley, 1975: 101. — Bridges, 1988: I.74, II.77. — Johnson and Matusik, 1988: 236. — Schwartz, 1989: 240.

DIAGNOSIS: Male tergite 8 with elongate dorsoterminal prong (diminutive lobe in *N. shoumatoffi*, shorter terminal prongs in mainland taxa *N. celona*, *N. milleri*, and *N. australivaga*); male genitalia with lateral lobes protruding about one–half the valvae length

(lobes nearly absent in *N. shoumatoffi*, greatly produced in mainland taxa). Female genitalia with caudal and cephalic ductal elements of about equal size (cephalic element diminutive in *N. shoumatoffi* and mainland taxa). Hindwing under surface with nearly complete, black medial band and with yellow Thecla spot (*N. shoumatoffi* with mottled, discontinuous band and black Thecla spot; mainland taxa with one or two continuous brown bands and yellow to orange Thecla spot).

DESCRIPTION: *Male.* Upper Surface of Wings: ground color brilliant iridescent azure blue from base to subapex, forewing with elliptic black androconial brand contiguous with black coloration of wing apex, hindwing with thin black marginal band. Under Surface of Wings: ground color chalky white; forewing with black postmedial line, costa to cell CuA1; hindwing with medial band of closely adjacent black slashes vividly contrasting the ground color, scattered black slashes in the postbasal area and light crenate black slashes along the outer margin; limbal area with Thecla spot yellow to orange-yellow and a central black dot. Length of Forewing: 11.5–13.0 mm. *Female.* Upper Surface of Wings: similar to those of male but with fuscous marginal areas more extensive and without forewing androconial brand. Under Surface of Wings: similar to those of males. Length of Forewing: 11.5–13.5 mm. *Male Tergal Morphology and Genitalia* (figs. 57, 60, 61). *Sipc* typical of genus but with dorsoterminal spine elongate (length exceeding three–fourths width of the tergite dorsum). Brush organs typical of genus. Genitalia with

TABLE 3

Characters *Nesiostrymon* and *Terra* Species and Species Groups Used for Figure 2 Cladogram Construction

(apomorphic (A) and plesiomorphic (P) states for characters of table 4 matrix; description and terminology as in table 1)

Tergal Morphology

1. Male, condition of tergite 8: (A) tergite 8 with specialized subcordate incised posterior cavity ("*sipc*" sensu Field, 1967a, 1967b; Johnson, 1988a) with dorsoterminal margin caudoventrally produced (figs. 57c, d, 60, 61, 63, 65, 66, 68); (P) tergite 8 unspecialized (without *sipc*) (figs. 58c, d, 69, 72, 73, 74, 78–80).

2. Male, condition of *sipc* terminus: (A) dorsoterminal margin of subcordate incised posterior cavity terminating in a caudoventrally directed lobe (not an elongate prong) (fig. 63); (P) dorsoterminal margin of tergite 8 entire.

3. Male, condition of *sipc* terminus: (A) dorsoterminal margin of subcordate incised posterior cavity terminating in an elongate, caudoventrally directed, prong (fig. 57c, d, 60, 65, 66, 68); (P) dorsoterminal margin of tergite 8 entire.

Genitalia

4. Male, configuration of valvae: (A) lateral margin of each valve with prominent terminally directed lobe (fig. 57a, b); (P) lateral margin of each valve generally entire (figs. 58, 84).

5. Male, condition of valve lateral margin: (A) lateral marginal lobe of each valve constricted to a point with length of lobe equal to or exceeding that of central valval lobe (figs. 65, 66, 68); (P) lateral marginal lobe not constricted, elongate or in any other way sculptured so as to equal or exceed the length of the central valval lobe (fig. 57a, b).

6. Male, condition of valvae central lobes: (A) central lobes tapered contiguously from valval base and paired in caudoventral one-third to one-fourth of valve length (figs. 63, 72); (P) central lobes paired from caudoventral one-half to entire valval length (figs. 84, 85a–c) [note: considering primitive condition, central lobe = caudal extension (fig. 57a)].

7. Female, configuration of ductus bursae: (A) respective opaquely sclerotized caudal and cephalic elements of ductus bursae connected by a smooth constricted and transparent neck (figs. 59, 62, 64, 67) (e.g., without "bulb"); (P) ductus bursae contiguous with opaque sclerotization (fig. 84).

8. Female, condition of cephalic ductal element: (A) contiguous opaquely sclerotized length of cephalic ductal element comprising not less than 0.4 that of contiguous opaquely sclerotized expanse of caudal ductal element (fig. 59); (P) ductus bursae with opaquely sclerotized "antrum" (figs. 84b, 85d sensu Klots, 1970) contrasting diminutive cephalic element of less than one-fourth ductus bursae length (figs. 84b, 85a, b, d).

9. Female, condition of juncture of caudal and cephalic ductal elements: (A) transparently sclerotized juncture of caudal and cephalic elements of ductus bur-

TABLE 3—(*Continued*)

sae with prominent, ventrally directed ovate sclerotized element (the "bulb," figs. 69, 70, 71, 75, 76, 77); (P) same area without bulb.

10. Female, condition of juncture of caudal and cephalic ductal elements: (A) sclerotized elements robust and divided into caudal and cephalic elements by a transparent central neck and adjacent sclerotized bulb (fig. 69); (P) sclerotized elements robust but contiguous and entire (fig. 84).

11. Female, condition of sclerotized bulb: (A) sclerotized bulb robust, widest ventral diameter equaling approximately half the length of cephalic ductal element and bulb occurring adjacent caudal end of cephalic half of the ductus bursae (fig. 69); (P) sclerotized bulb robust as above [note: as opposed to character 12 (A), maximal ventral bulb diameter less than one-fifth length of cephalic ductal element in apotypic *Terra* (fig. 2, taxa 5, 6)] and occurring adjacent the cephalic end of the cephalic half of the ductus bursae (fig. 84).

12. Female, condition of caudal and cephalic ductal elements: (A) cephalic ductal element elongate and thin, length equaling or exceeding five times maximal ventral diameter of bulb; bulb located in caudal half of entire ductus length (figs. 70, 71, 75–77); cephalic ductal element robust, length approximately two times maximal ventral diameter of bulb; bulb located in cephalic half of entire ductus length (fig. 69).

Wing Pattern

13. Both sexes, pattern of under surface: (A) under surface of hindwing with postmedial pattern elements colored golden yellow and occurring disjunctly in each cell from SC + R1 at least cell CuA2 and of about even expression (figs. 38, 40); (P) under surface of hindwing with postmedial pattern element in cell RS obsolescent to lacking, causing postmedial band to appear basally directed from vein M2 to the costa (figs. 34, 36).

14. Both sexes, pattern of under surface: (A) under surface of forewing and hindwing with pattern elements variously congealed into thickened lines or bands and colored yellow-orange, yellow-brown, brown, or red (figs. 42, 44, 46, 48, 50, 52, 54, 56); (P) see entry 13(A).

vinculum smooth and lacking ventral spurs. Valvae with lateral winglike lobes widely elliptical but short (distal expanse only about one–half the length of the valval termini); lateral margins of lobes variously produced in allopatric subspecies. Saccus robust, length about equal to caudoventral expanse of vincular arc (fig. 57). Aedeagus typical of genus but with caecum more prominent than congeners (comprising up to one–fifth aedeagal length) and terminus less recurvate. *Female Tergal Morphology and Genitalia* (fig. 59). Tergite 8 typical of genus. Papillae anales with

TABLE 4
Character State Matrix for *Nesiostrymon* and *Terra* Ingroup
(columns 1–14, characters enumerated in table 3; rows as enumerated below[a, b])

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
A	1	0	1	1	1	0	1	0	0	0	0	0	0	0
B	1	0	1	1	0	0	1	1	0	0	0	0	0	0
C	1	1	0	0	0	1	1	0	0	0	0	0	0	0
D	0	0	0	0	0	1	0	0	1	1	1	0	0	0
E	0	0	0	0	0	0	0	0	1	0	0	1	1	0
F	0	0	0	0	0	0	0	0	1	0	0	1	0	1
L	0	0	0	0	0	0	0	0	0	0	0	0	0	0

[a] Taxa A–F. (A) *N. celona/milleri/australivaga,* (B) *N. celida,* (C) *N. shoumatoffi,* (D) *T. hispaniola,* (E) *T. tera,* (F) *T. andevaga/chilica/calchinia/cana.*

[b] L, Characters used for Lundberg rooting of parsimonious network based on monophyly of *Nesiostrymon* and *Terra* in figure 1, tables 1 and 2.

terminus more lobate than congeners. Genitalia with lengths of respective opaque ductal elements generally similar, cephalic ductal element length comprising not less than two–fifths of the respective caudal element; terminal ductal opening narrow, edged with thin lamellal lips.

TYPE: Deposition uncertain. Comstock and Huntington (1958–1964 [1955]) and Bridges, 1988 speculated BMNH but this is unconfirmed (P. R. Ackery, BMNH, personal commun.) and I have not found it there. The name, however, is unambiguous. Type Locality: Cuba.

DISTRIBUTION (fig. 81): Cuba, Hispaniola, and Puerto Rico confined to dense mesic forests and their immediate margins (see Biogeography).

Allopatric Island Endemics of
N. celida in the Antilles

As noted under the generic entry, interisland subspecies have been traditionally employed by lepidopterists and these populations often have biogeographically informative characters. Hitherto, only the Cuban and Puerto Rican populations of *N. celida* have been characterized and names have not been available for the Hispaniolan elements. Interisland endemics are reviewed below in an abridged descriptive format. A new subspecies is described from the southern Hispaniolan paleoisland. Subspecies of *N. celida* differ negligibly in the female genitalia but have distinctive characters of the wings and in the tergal and valval structures of males.

Nesiostrymon celida celida (Lucas)
Figures 3–6, 57, 60

CHARACTERIZATION: Black apices of forewings broad, completely encompassing the male forewing brands (fig. 3); male genitalia (fig. 57, 60a–d) with lateral valval lobes protruding at near right angles to the central valval lobes with little, if any, marginal production.

TYPES: See generic treatment.

DISTRIBUTION (fig. 81): Restricted to Cuba; mainly known from old material with data suggesting mesic forest habitats typical of the species elsewhere.

MATERIAL EXAMINED: *N. c. celida*: CUBA. Guantanamo (1♂, 1♀) (AMNH); Holquin (2♂) (AMNH); "Cuba" (6♂, 2♀) (BMNH); "Cuba" leg. Poey (2♂) (CMNH); Santiago (1♂) (BMNH); Bayate (1♂) (BMNH); Guantanamo (1♀) (BMNH); no data [with Cuban specimens] (2♀) (BMNH); "Cuba" (2♂, 2♀) (MNHN); Cotorro, 1884 (1♂) (MNHN); "Cuaba" [sic] (one male) (MNHN); Guantanamo (1♂, 1♀) (MNHN).

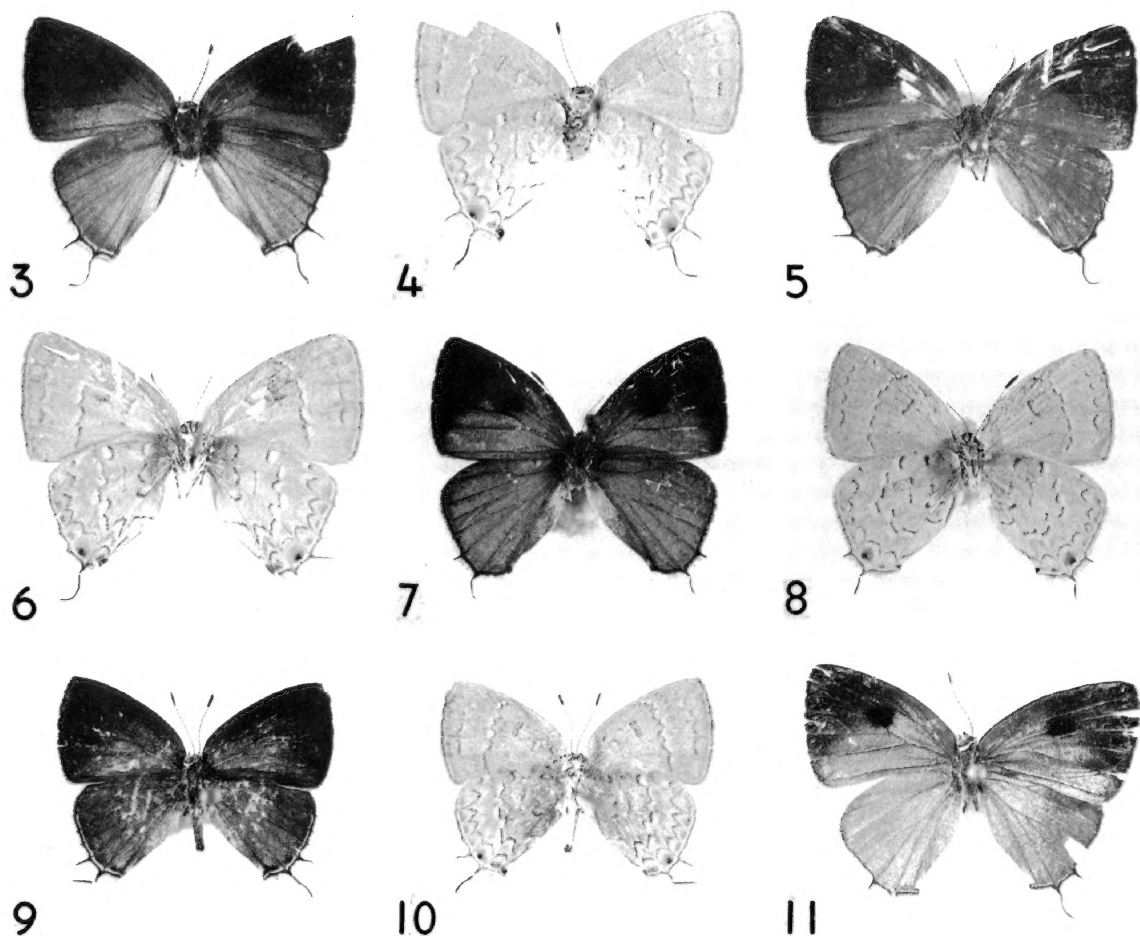### *Nesiostrymon celida aibonito* (Comstock and Huntington)
Figures 7–12, 60, 61

Thecla celida aibonito Comstock and Huntington, 1943: 76.

CHARACTERIZATION: Forewing apex darkened only at apex, leaving male forewing brand surrounded by iridescent blue (figs. 7, 11). Lateral lobe of male genitalia with slightly produced sclerotized ridges (figs. 60c, 61e, f).

Figs. 3–11. Adults of *Nesiostrymon*. *N. c. celida*: **3, 4.** Upper surface, under surface, male, Guantanamo, Cuba (AMNH); **5, 6.** Upper surface, under surface, female, same data (AMNH). *N. c. aibonito*: **7, 8.** Upper surface, under surface, holotype male; **9, 10.** Upper surface, under surface, allotype female; **11.** Upper surface, male, Polo, Barahona Prov., Dominican Republic (AMNH).

TYPES: Holotype male, AMNH labeled "Thecla celida aibonito Comstock and Huntington, holotype male," "holotype," "Aibonito, P.R., July 14–17, '14." Type Locality: Aibonito, Puerto Rico.

DISTRIBUTION (fig. 81): Known from mesic forest in Puerto Rico and on Hispaniola in regions on, or directly adjacent to, the northern palaeoisland.

MATERIAL EXAMINED: In addition to types listed above—DOMINICAN REPUBLIC. Broadleaf Cloud Forest, 19 km N Cabral, Barahona Province, June 29, 1985, leg. K. Johnson and D. Matusik (2♂) (AMNH); Bamboo Hole Canyon, nr. Jarabacoa, La Vega Prov., June 23, 1985, leg. K. Johnson; "Domingo" (1♂, 2♀) (BMNH). Unexamined material listed by Schwartz (1989, sexes not noted) (included in fig. 81): 14 km SW Jamao al Norte, 534 m, Espaillat Prov. (one); 1 km S Constanza, La Vega Prov. (one); 16 km NE La Romana, 61 m, La Altagracia Prov. (one). PUERTO RICO. See Types entry above; Aibonito, Puerto Rico, July 14–17, 1914 (paratype male) (AMNH).

Nesiostrymon celida baorucoensis,
new subspecies
Figures 13–16, 59, 60

CHARACTERIZATION: Male forewing brand and black apex conjoined like the nominate but with lateral lobes of male valvae greatly produced along their distal margins.
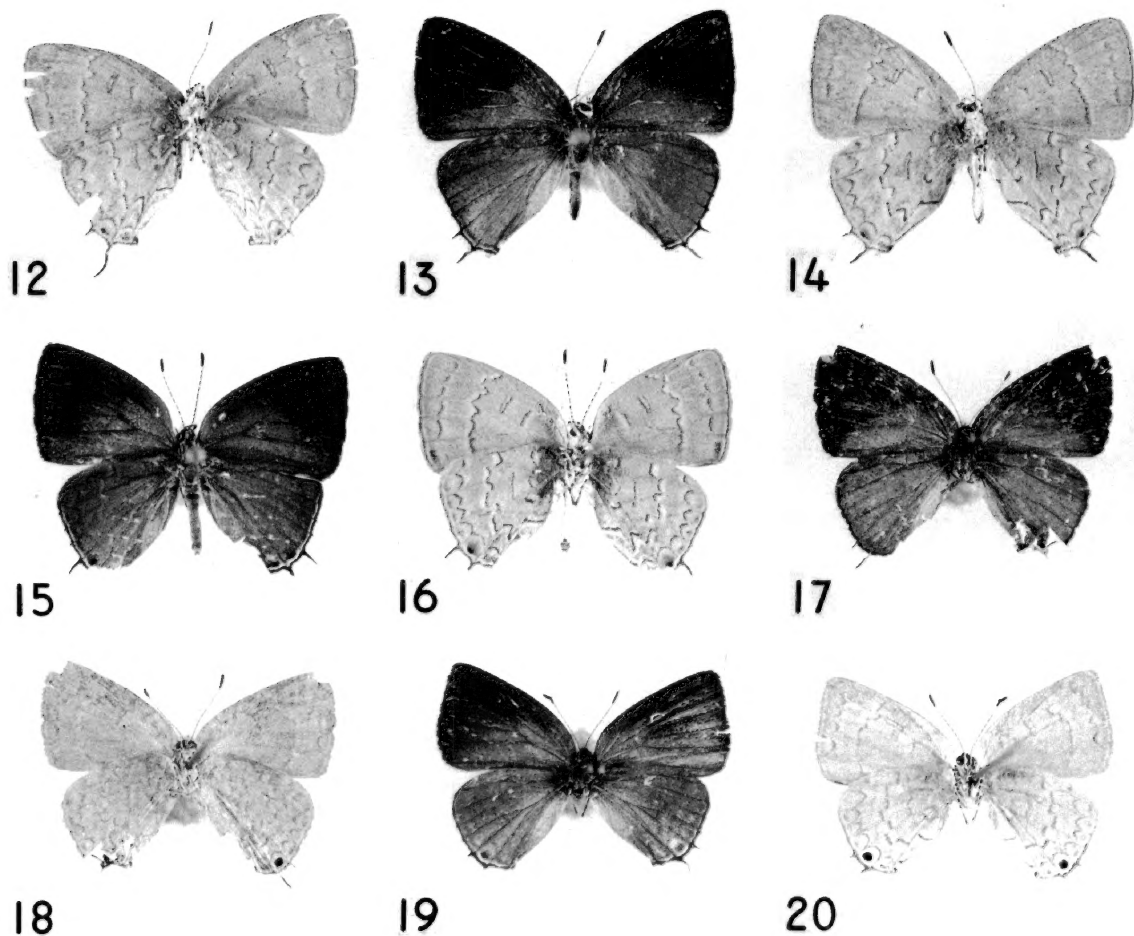
Figs. 12–20. Adults of *Nesiostrymon*. *N. c. aibonito*: **12.** Under surface, male of figure 11. *N. c. baorucoensis*: **13, 14.** Upper surface, under surface, holotype male; **15, 16.** Upper surface, under surface, allotype female. *N. shoumatoffi*: **17, 18.** Upper surface, under surface, holotype male; **19, 20.** Upper surface, under surface, allotype female.

DESCRIPTION: *Male.* Upper Surface of Wings: ground color brilliant iridescent azure blue; forewing with brand and black apical color conjoined; hindwing with long tail, terminus vein CuA2, short tail, terminus vein CuA1. Under Surface of Wings: ground color dingy bluish gray; forewing with black postmedial line, costa to cell CuA1; hindwing with medial band of nearly conjoined black slashes, a discal and two to three black postbasal slashes and a light blackish crenate line along the outer margin; limbal area with small, orangish Thecla spot. Length of Forewing: 9.5–12.5 mm. *Female.* Upper Surface of Wings: similar to male but with fuscous marginal areas more extensive and without forewing brands. Under Surface of Wings: as on males.

Length of Forewing: 10.0–12.5 mm. *Male Tergal Morphology and Genitalia* (fig. 60b, 61g). Typical of species (fig. 61) but with greatly produced lateral valvae lobes. *Female Tergal Morphology and Genitalia* (fig. 59). Differing negligibly from the nominate.

TYPES: Holotype male, allotype female, "Upper Abejas" (sensu Johnson and Matusik, 1988), July 5–17, 1986, deposited AMNH. Paratypes. AMNH: "Las Abejas" (see Remarks) July 1, 1984 (1♂); July 5–17, 1986 (18♂, 14♀); CMNH: same data but July 13–18, 1987 (3♂, 3♀); AME: same data but June 30–July 3, 1988 (10 specimens); DMC: same data but July 1–5, 1984 (3♂, 2♀); July 5–17, 1986 (5♂, 4♀); June 29–July 3, 1988 (4♂, 4♀).

DISTRIBUTION (fig. 81): Known only from mesic broadleaf deciduous forest in deep ravine areas of the Sierra de Baoruco uplands (1150–1200 m) in the southwestern Dominican Republic. Extremely habitat restricted, occurring only in areas of filtered sunlight in dense wet woods; to date collected in numbers almost exclusively while perching on *Gyrotaenia* Grisebach (Urticaceae) (see Biogeography).

REMARKS: This name is needed for the southern Hispaniolan subunit of the Antillean distribution of *Nesiostrymon*. Johnson and Matusik (1988) first commented on the field behavior of *N. celida* based on populations located in the southwestern Dominican Republic (see Biogeography). Along with the structural characters differentiating *N. celida* subspecies, medial under surface stripes are generally continuous in *N. c. baorucoensis* and *N. c. celida* and disjunct in *N. c. aibonito*. It should also be noted that variation in forewing length in *N. c. baorucoensis* is probably attributable simply to the large sample size.

ETYMOLOGY: Refers to the Sierra de Baoruco of Hispaniola.

MATERIAL EXAMINED: In addition to types listed above—DOMINICAN REPUBLIC. Unexamined material listed by Schwartz (1989) (included in fig. 81): 4–7 km NE El Aguacate, 519–824 m, Independencia Prov. (2); 1 km SE Banano, 143 m, Pedernales Prov. (2); Las Abejas, 11 km NW Aceitillar, 1220 m, Pedernales Prov. (1); 1 km N Aceitillar, 1281 m, Pedernales Prov. (1).

Nesiostrymon shoumatoffi
(Comstock and Huntington),
revised status
Figures 17–20, 62, 63

Thecla celida shoumatoffi Comstock and Huntington, 1943: 75; 1958–1964 [1963]: 119. — Kaye, 1931: 535, pl. 39, fig. 10. — Schwartz, 1989: 240.
Nesiostrymon celida shoumatoffi: Clench, 1964: 248, 251. — Brown and Heinemann, 1971: 4; 1972: 232. — Scott, 1986: 21. — Riley, 1975: 101. — Bridges, 1988: I.319, II.77. — Johnson and Matusik, 1988: 236.

DIAGNOSIS: Male tergite 8 terminating in small protruding dorsal lobe; genital valvae with little lateral production. Female genitalia cephalically recurvate and with caudal lamellae distally pronged. Wing under surfaces with all markings disjunct and lineal; Thecla spot black.

DESCRIPTION: *Male.* Upper Surface of Wings: ground color iridescent sky blue, forewing with small, elliptic androconial brand contiguous with black wing apex; hindwing with thin black marginal band, long tail, terminus vein CuA2, short tail, terminus vein CuA1. Under Surface of Wings: ground color bright white; forewing with thin, black postmedial line of disjunct dashes, costa to cell CuA1; hindwing with medial band of thin black dashes, lightly marked discal and postbasal dashes and disjunct crenate markings along the outer margin; limbal area with small black Thecla spot. Length of Forewing: 10.0–11.5 mm. *Female.* Upper Surface of Wings: marked as male but without forewing brand. Under Surface of Wings: marked as male but with yellow occasionally surrounding Thecla spot. Length of Forewing: 10.0–11.5 mm. *Male Tergal Morphology and Genitalia* (fig. 63). *Sipc* with dorsal terminus short, limited to a terminally protruding lobe. Brush organs typical of genus. Genitalia with vincular margin entire, lacking ventral spurs. Valvae with lateral, winglike lobes occurring only as rounded keels distad valval termini; central valval lobes produced, tapering a concave terminus with short distal prongs. Extravalvular element more elongate than in congeners. Saccus elongate, length exceeding caudoventral expanse of vincular arc. Aedeagus elongate, nearly three times caudoventral expanse of vincular arc, and with shaft curvate; caecum comprising one-seventh or less of aedeagal length. Flat valval ventrum more similar to *Terra* than to congeners (see Discussion below). *Female Tergal Morphology and Genitalia* (fig. 62). Tergite 8 typical of genus. Papillae anales with thick, marginally incised, lateral sclerotizations and pointed terminus. Genitalia with caudal element of ductus bursae greatly elongate (exceeding length of cephalic element by four to five times) and with cephalic element curvate; terminal lamellae flared widely and distally pronounced into two terminally directed prongs. Overall genital shape and terminal elements more reminiscent of mainland *N. celona* than Antillean *N. celida* (see Discussion below).

TYPES: Holotype male, allotype female, AMNH, respectively labeled "Thecla celida shoumatoffi Comstock and Huntington, holotype male," "holotype," "Christiana, Jamaica, 26 vii 1933," "collectors A. Avinoff and N. Shoumatoff;" same, but "July 26 1933 [sic]." Type Locality: Christiana, Jamaica.

DISTRIBUTION (fig. 81): Primarily Jamaican uplands (Blue Mountains and Cockpit country) in deciduous forest and forest openings (see Discussion).

DISCUSSION: Hitherto, based on simple wing pattern comparison, this species had been considered a subspecies of N. celida (Clench, 1964; Riley, 1975; Schwartz, 1989). However, when wing pattern and morphology are considered in context with all congeners, it is clear that N. shoumatoffi is a distinct species. The male tergite 8 and genital valves exhibit a primitive condition. Flat ventral surfaces on the valvae resemble sister genus Terra; overall shapes of the female ductus bursae and male aedeagus are similar to those in mainland congener N. celona. As a result, species status for N. shoumatoffi appears unequivocal, irrespective of the systematic method used to cluster taxa of the group.

Brown and Heineman (1972) noted the "rarity" of N. shoumatoffi. Historical records primarily indicate upland deciduous forest habitats and surrounding margins; some old specimens have data suggesting more lowland locales and may not be reliable. As with N. celida, small historical samples likely result from collectors not locating the species' microhabitat. Remarks in Brown and Heineman (1972) recorded the species from "bushes." The latter may be Gyrotaenia, noted heretofore as the perching substrate for N. celida.

MATERIAL EXAMINED: In addition to types listed above—JAMAICA. Newcastle (2♂) (BMNH); "Jamaica" (1♂) (BMNH); "Jamaica," 1914, leg. Avinoff (1♂) (CMNH); Flamstead, 1883, 3900 ft (AME); Allsides, July 26, 1933, leg. "A & S" (1♂) (CMNH); Low River at Trelawny, July 30, 1933 (3♂, paratypes) (CMNH); Christiana, July 26, 1933, leg. Avinoff and Shoumatoff (4♂, paratypes) (CMNH); Coleyville, Manchester, July 29, 1933 (5♂, paratypes) (CMNH); Moneague, St. Ann's, July 21, 1933 (6♂) (CMNH); Mt. Diablo, July 10, 1936 (9♂); "Jamaica" (1♀)

(MNHN); Wilson Run, Trelawny Parish, June 29, 1951, leg. H. Heineman (1♀) (AMNH); Polly Ground, track to Bat Cave, 6 February 1957, leg. H. Heineman (1♀) (AMNH). Listed by Brown and Heineman (1972) but not located in this study: St. Thomas, Corn Puss Gap, July 12, 1949, leg. "I.J.," Cuna Cuna, July 15, 1933 (sighted), leg. Avinoff and Shoumatoff; St. Catherine, Bog Walk at Flat Bridge, June 7, 1959, leg. Bengry.

MAINLAND TAXA

Nesiostrymon celona (Hewitson), new combination
Figures 21–26, 64, 65

Thecla celona Hewitson, 1863–1878 [1874]: 179. — Comstock and Huntington, 1958–1964 [1959]: 181. — Bridges, 1988: I.75, II.77. — Johnson and Matusik, 1988: 236.

DIAGNOSIS: Upper surface ground color in males dark azure blue with lustrous black ovate brand dominating distal end of forewing discal cell; female dull blue to brownish. Under surface of both sexes with wide, continuous, lunular orange-brown medial bands extending across forewing and hindwing. Male genitalia with lateral lobes elongate (length equaling that of central valval lobes) and tapering to pointed termini. Compared to insular mainland congeners N. milleri and N. australivaga, N. milleri with under surface bands discontinuous, a unique postbasal band and male genitalia with elliptic valval lobes flanked by lobate vincular spurs; N. australivaga with under surface bands straight, thin, basally directed and suffused, male genitalia with diminutive lateral lobes and female genitalia robust as in N. celida.

DESCRIPTION: Male. Upper Surface of Wings: ground color dark iridescent azure bordered by black margins, apices and subapices. Forewing with lustrous black androconial brand outstanding over azure ground color; hindwing with long tail at vein CuA2 terminus, short tail at vein CuA1 terminus. Under Surface of Wings: ground color distally light gray, basally gray-brown, divided on both wings by a lunular (sometimes jagged) orange-brown medial band bordered distally with black; submargins on both wings with white-edged brown dashes occurring in
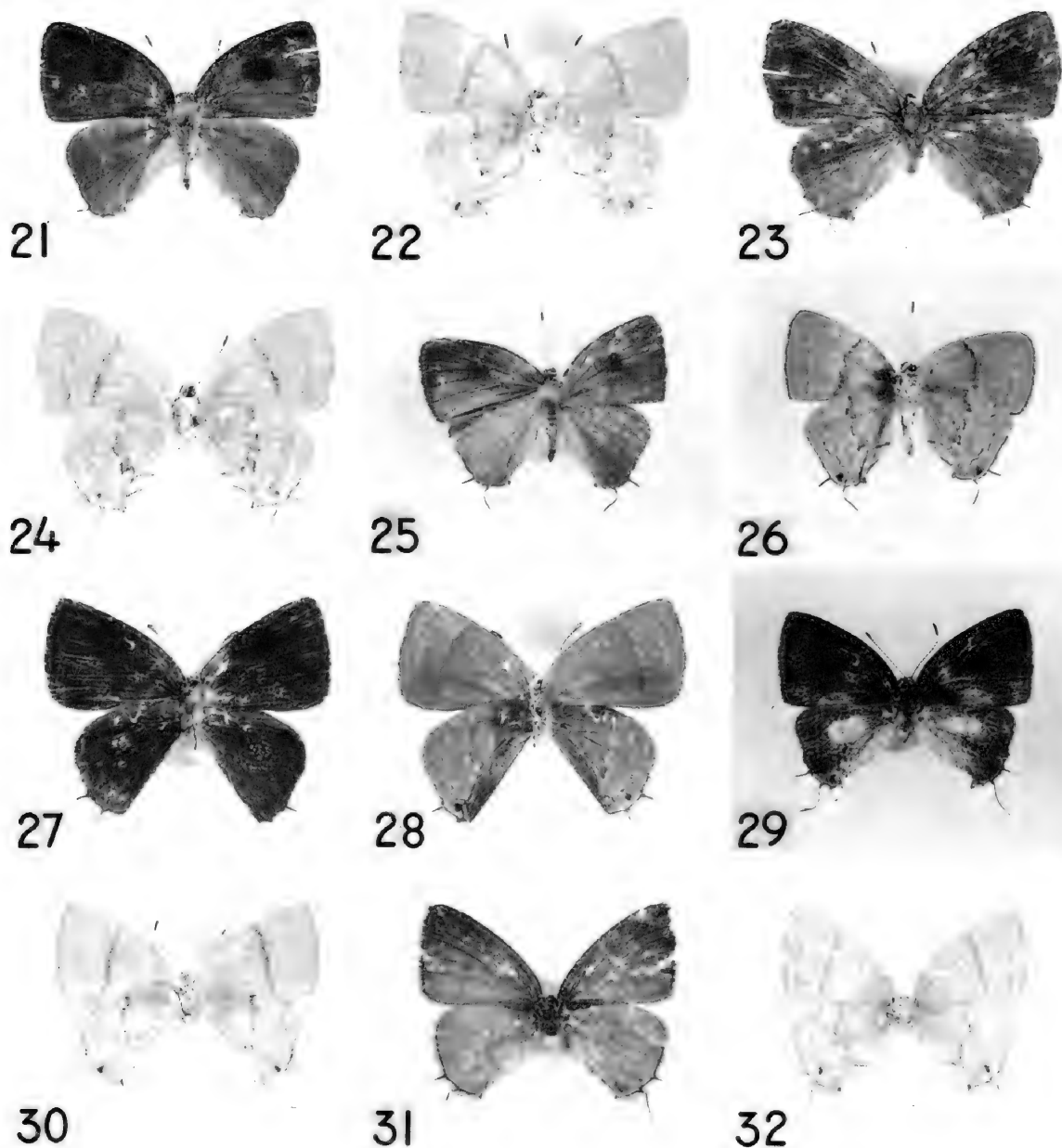
Figs. 21–32. Adults of *Nesiostrymon*. *N. celona*: **21, 22.** Upper surface, under surface, topotype male; **23, 24.** Upper surface, under surface, topotype female; **25, 26.** Upper surface, under surface, male, Jalapa, Mexico (AMNH). *N. milleri*: **27, 28.** Upper surface, under surface, holotype male. *N. australivaga*: **29, 30.** Upper surface, under surface, holotype male; **31, 32.** Upper surface, under surface, allotype female.

each cell; limbal area with small orange to brownish Thecla spot. Length of Forewing: 8.0–11.0 mm. *Female*. Upper Surface of Wings: ground color dull iridescent blue to brownish; fuscous marginal areas more extensive than in males and forewings lacking brands. Under Surface of Wings: similar to that of males but with bands more pronounced and often more jagged. Length of Forewing: 9.0–11.0 mm. *Male Tergal Morphology and Genitalia* (fig. 65). *Sipc* with dorsoterminal prong of moderate length (slightly
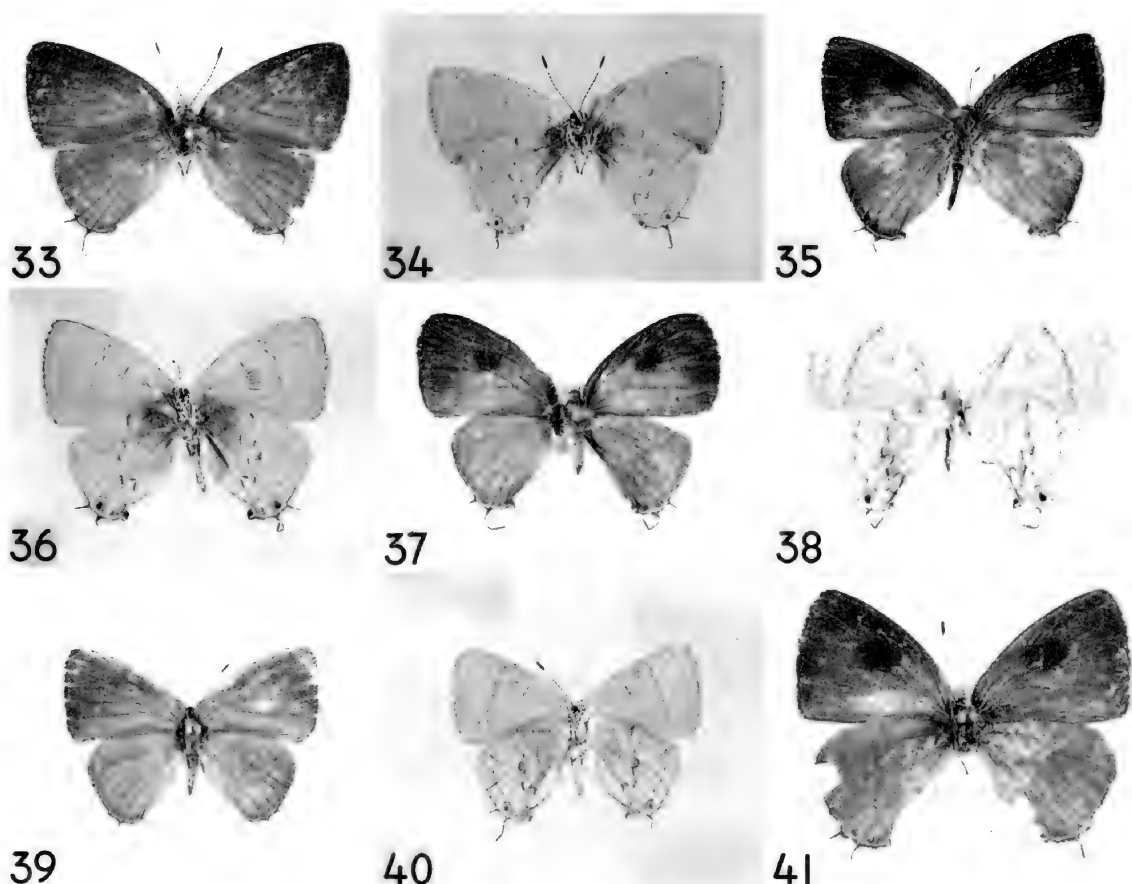
Figs. 33–41. Adults of *Terra*. *T. hispaniola*: **33, 34.** Upper surface, under surface, allotype female; **35, 36.** Upper surface, under surface, male, "Middle Abejas," Pedernales Prov., Dominican Republic, July 30, 1990, leg. D. Matusik (AMNH). *T. tera*: **37, 38.** Upper surface, under surface, topotype male; **39, 40.** Upper surface, under surface, topotype female. *T. andevaga*: **41.** Upper surface, holotype male.

exceeding one-half the tergite dorsum width). Brush organs typical of genus. Genitalia with vincular margins smooth, lacking ventral spurs. Valvae with lateral lobes steeply pointed and lengths ranging from four-fifths to equal that of the central valval lobes. Saccus robust, shorter than most congeners, with length usually less than that of vincular arc. Aedeagus elongate as typical of genus and recurvate in the terminal one–third, caecum comprising only one-seventh to one-eighth aedeagal length. *Female Tergal Morphology and Genitalia* (fig. 64). Tergite 8 typical of genus. Papillae anales with pointed terminus typical of mainland congeners. Genitalia with ductus bursae more fluted than in congeners, transparent neck restricted and located relatively close to a swollen cephalic terminus. Lateral edges of ductus bursae terminus pro-

duced, forming a pair of terminally directed prongs as in *N. shoumatoffi* and *N. australivaga*.

TYPES: Holotype male, BMNH, labeled "Espiritu Santo, Hewitson Coll. 79–69. Thecla celona. 1.," "male, Thecla Type celona," "B.M. Type No. Rh. 981." Type Locality: Espiritu Santo, Brazil.

DISTRIBUTION (fig. 81): From east central Mexico southward, excluding the Amazon basin, to southeastern Brazil and central Peru.

DISCUSSION: There is remarkably little variation in the male and female morphology of specimens from central Mexico southward to southeastern Brazil. There appears to be little doubt that all these populations represent the same species (figs. 25, 26). Though this character homogeneity is in marked contrast to similarly distributed populations of

Terra (see below), there are distinctive mainland congeners of *Nesiostrymon* occurring sympatric with *N. celona* on the Guyana Shield (*N. milleri*, below) and in montane central Argentina (*N. australivaga*, below).

Contrasting Antillean congeners, but paralleling the historical records of *Terra* species, females of mainland *Nesiostrymon* taxa are poorly known. However, their characters figure heavily in the evaluation of relationships (figs. 1–2, tables 1–4). Because of jagged under surface bands, black and white photos of some *N. celona* females may resemble either sex of certain species of *Caerofethra* Johnson, particularly *C. iambe* (Godman and Salvin) (fig. 84). However, the under surfaces of *Caerofethra* taxa have tawny ground colors and bright orange wing bands.

MATERIAL EXAMINED: In addition to type listed above—BOLIVIA. Rio Surutu, April 1915 (1♂), October 1913 (1♂) (both CMNH); Rio Yapacani, 600 m, Sept. 1914 (1♂) (CMNH); Rio Yapacani, E. Bolivia (1♂) (CMNH). BRAZIL. Gavea, Paraná, 1 February 1930 (1♂) (MPM); Amazonas, Tonantins, July–September 1880, leg. de Mathan (1♂) (BMNH); Santarém, December 20, 1922, leg. C. S. Larsen (MNHN). COLOMBIA. Cali, Cauca, April 3, 1909, leg. Paines and Brinkley (1♂) (BMNH); Novelle Granada, leg. de Methan, September 15, 1990 (1♀) (BMNH); Cauca, Cali, April 3, 1909, Paines and Brinkley (1♂) (BMNH); Puerto Colombia, July 11–12, 1920, dry scrub area (1♂) (CMNH). ECUADOR. Baños, 1800 m, Tungurahua, July 1936 (1♂) (BMNH); Puyo, Napo, 1000 m December 14, 1938 (1♂) (BMNH); Balzapamba (1♂) (BMNH). MEXICO. Catemaco, Veracruz, May 1961, leg. Escalante (1♂) (AME); Yucatan, Piste, July 15, 1959, leg. E. C. Welling (2♂) (CMNH); Yucatan, Quintana Roo, leg. E. C. Welling, November 17, 1955 (1♂) (CMNH); Colima (1♂, 1♀) (CMNH); Colima (1♂) (HEC); S. Mexico, leg. Townsend (1♂) (CMNH); Quintana Roo, Yucatan, November 17, 1957, leg. Welling (1♂) (CMNH); Presidio, April 1940, leg. Hoffman (♂) (AMNH); Catemaco, May 1961 (♂) Escalante (AMNH); Piste, Yucatan, August 15, 1960 (2♂) (AMNH); "locality 5092," Moeck (1♂) (MPM); Chiapas, leg. Hoffman (1♂) (AMNH). PANAMA. Summit, Canal Zone, May 3, 1964, leg. Shull (1♂) (CMNH). PERU. Iqui-

tos, leg. E. May (1♂) (BMNH); Tarapota (1♂) (BMNH).

Nesiostrymon milleri, new species
Figures 27, 28, 66

DIAGNOSIS: Upper surface iridescent blue darkest of congeners, with male forewing brands located more distally and obscured by the iridescent ground basad thin black apical borders. Under surface with an iridescent blue sheen over gray ground color; hindwing with postbasal line paralleling the medial band and ground color between these distinctly darker gray than rest of wing. Male genitalia with lateral lobes widely elliptical, length about three-fourths that of central valval lobe; vinculum with unique ventrolateral spurs.

DESCRIPTION: *Male.* Upper Surface of Wings: ground color deep iridescent navy blue; forewing with blackened androconial brand located at extreme distal end of discal area; hindwing with long tail at vein CuA2 terminus, short tail at vein CuA1 terminus. Under Surface of Wings: ground color dull gray with iridescent blue sheen; forewing with discontinuous black postmedial line, costa to cell CuA1. Hindwing with discontinuous black medial band paralleled by a prominent black discal line extending from cell RS to CuA1 and suffused basally with dark brown. Submargin with white dashes in each cell; limbal area with black Thecla spot slightly bordered with orange. Length of Forewing: 10.0 mm (holotype). *Female.* Unknown. *Male Tergal Morphology and Genitalia* (fig. 66). *Sipc* typical of genus but with dorsoterminal prong robust, moderate in length (length two times maximal width) and blunt at terminus. Brush organs typical of genus. Genitalia with ventrolateral margin of vinculum marked by prominent spurs overlapping ventroterminal surface of valvae. Valvae with lateral lobes winglike, with elliptical termini, lengths exceeding three-fourths that of the central valval lobes. Saccus robust, length about equal to that of vincular arc. Aedeagus robust, length exceeding rest of genitalia by only about one-fifth, caecum comprising about one-fifth the length and undulate in terminal one-half.

TYPES: Holotype, male, Aragua, Portochuelo Pass, Parque Nacional Henri Wittier, (Rancho Grande) Cloud Forest, July 24, 1981,

Station VE10, Venezuela, leg. Lee D. Miller, deposited AME.

DISTRIBUTION (fig. 81): Known only from the type locality.

DISCUSSION: Apparent insular occurrence of *N. milleri* reflects a distribution pattern seen in numerous recent revisionary studies of Neotropical hairstreak genera—a species of limited distribution on the Guyana Shield sympatric there with a congener of much wider geographic range (Johnson 1988a, 1989a, 1989b, 1989e).

ETYMOLOGY: Patronym for Lee D. Miller, who collected the type.

Nesiostrymon australivaga, new species
Figures 29–32, 67, 68

DIAGNOSIS: Males with upper surface fuscous wing borders extremely wide, obscuring the forewing brands; females brown. Under surface medial bands thin, straight, and basally directed. Male genitalia with central and lateral valval lobes diminutive; female genitalia with tapered configuration like *N. celona* but relative size of ductal elements resembling that of *N. celida* (see below).

DESCRIPTION: *Male.* Upper Surface of Wings: ground color darkly suffused iridescent blue bordered by wide blackened apices and subapices obscuring the ovate forewing brands. Hindwing with long tail at vein CuA2 terminus, short tail at vein CuA1 terminus. Under Surface of Wings: ground color gray-brown; forewing with thin, straight, basally directed brown medial band; hindwing with similar, very lineal band; limbal area with prominent yellow-orange Thecla spot marked centrally with black dot. Length of Forewing: 9.0 mm (holotype). *Female.* Upper Surface of Wings: ground color darkly suffused brown with wide, blackened apices and subapices and no forewing brand. Under Surface of Wings: similar to that of males. Length of Forewing: 10.0 mm (allotype); 10.0 mm (paratype). *Male Tergal Morphology and Genitalia* (fig. 68). *Sipc* typical of genus but with length of dorsoterminal prong slightly exceeding that of *N. celona* and with base of prong greatly produced and then tapered steeply to a sharp terminus; lateral edges of prong with prominent microtrichia. Genitalia with valval central and lateral lobes di-

minutive and lateral aspect robust. Saccus robust, more elongate than in *N. celona* (exceeding length of vincular arc). Aedeagus elongate as typical of genus and terminally curvate, caecum comprising about one-sixth aedeagal length. Brush organs typical of genus. *Female Genitalia* (fig. 67). Ductal elements tapering as in *N. celona* but with length of caudal element slightly more than twice that of cephalic element (caudal/cephalic ratio 0.55); cephalic element with slight dorsal inclination. Ductal terminus with short, terminally directed, lateral prongs as in *N. celona* and *N. shoumatoffi.* Papillae anales typical of mainland congeners.

TYPES: Holotype male, allotype female, "Mendoza, Argentina" (see Discussion below), ex. C. S. Larsen Collection, deposited MNHN. Paratype. MNHN: same data as primary types (one female).

DISTRIBUTION (fig. 81): Known only from "Mendoza" in Argentina (see Discussion below).

DISCUSSION: Recent studies of temperate zone South American Theclinae indicate a distinctive endemic fauna (Johnson, 1988a, 1989a, 1989b, 1989e; Johnson et al., 1988, 1990). Representatives of this fauna derive both from recent collections and ill-studied samples forwarded by early workers to various European museums. Notable among these are Argentine, Patagonian, and Chilean collections by C. S. Larsen and R. Martin at the MNHN and Argentine collections by K. Hayward and E. Giacomelli at the BMNH. The types of *N. australivaga* derive from the C. S. Larsen material. As detailed by Johnson (1989e, in press), MNHN curator Percy Lathy described several species from early C. S. Larsen material. However, many other austral specimens were never incorporated into the MNHN collection. Johnson et al. (1990) have noted that "Mendoza" data on C. S. Larsen specimens may not correspond to the current Mendoza Province of Argentina. Specific localities listed on Larsen labels including the notation "Mendoza" include sites north to modern La Rioja Province and south to Rio Negro Province.

ETYMOLOGY: The suffix *vaga* ("roamer") is added to the geographic term "austral," referring to the southerly occurrence of the species.
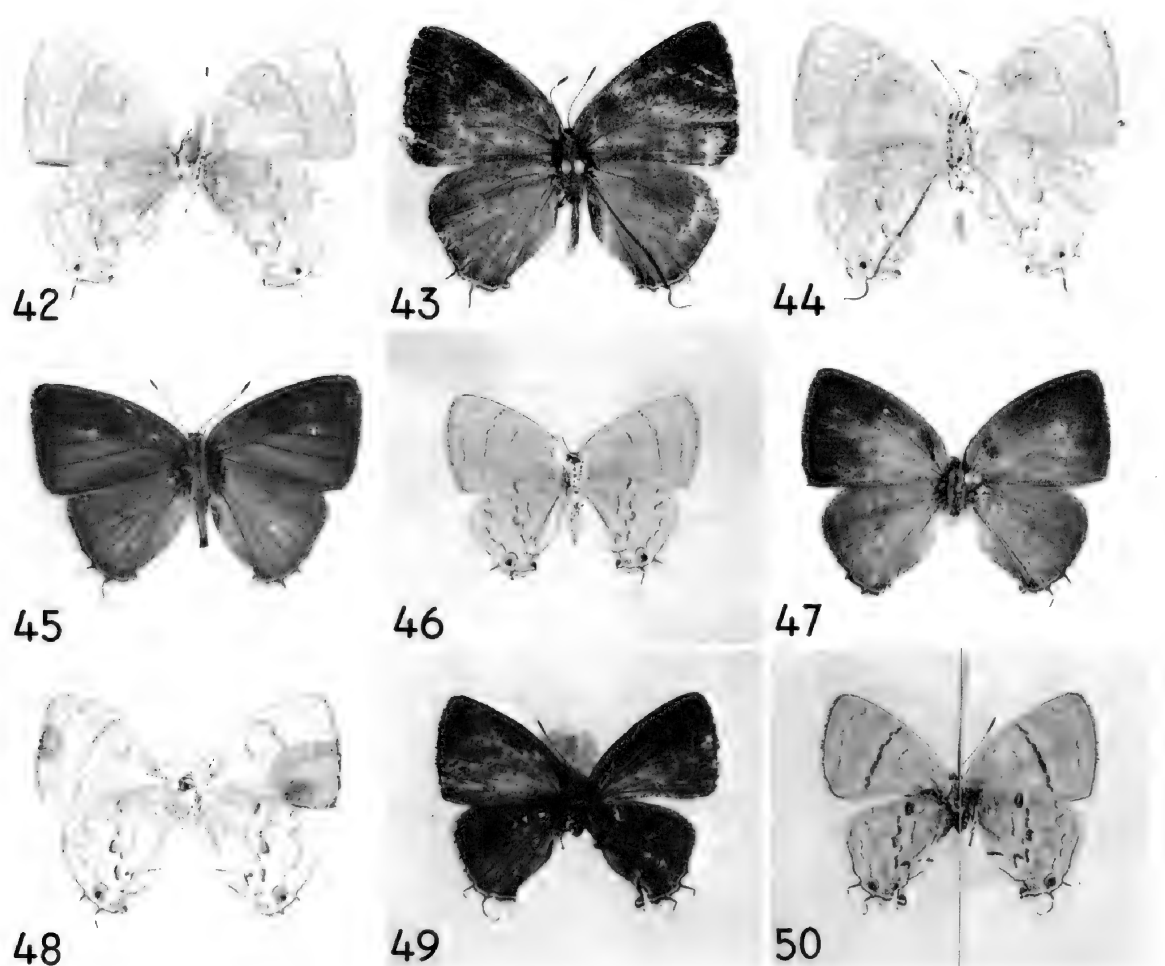
Figs. 42–50.   Adults of *Terra*. *T. andevaga*: **42.** Under surface, holotype male; **43, 44.** Upper surface, under surface, allotype female. *T. cana*: **45, 46.** Upper surface, male, "Tucumán," leg. Steinbach, (BMNH); under surface, male, "El Paraiso," Tucumán Province, Argentina, December 31, 1987, leg. R. Eisele (AMNH); **47, 48.** Upper surface, under surface, female, Villa Nougues, Tucumán Province, January 21, 1931, leg. K. J. Hayward (IML). *T. calchinia*: **49, 50.** Upper surface, under surface, male, Ega, Brazil (BMNH) [black and white reproduction of color slide].

GENUS *TERRA* JOHNSON AND MATUSIK
Figures 33–56, 58, 69–80

Terra Johnson and Matusik, 1988: 235. — Schwartz, 1989: 241.

DIAGNOSIS: Compared to all Eumaeini, female genitalia with an outstanding, ventrally directed, sclerotized bulb (figs. 69–80) attached to the transparent neck of the ductus bursae. Compared to *Nesiostrymon*, male tergite 8 without *sipc* and with genital valvae uniplanar and ventroterminally flat. Hindwing under surfaces with medial bands of yellow, orange, brown or red, not black as in *Nesiostrymon*.

DESCRIPTION: *Adult*. Body blackish, covered with gray to bluish hairlike microtrichia; eyes ringed with white; antennae black, finely striped with white. *Male*. Upper Surface of Wings: ground color dull iridescent blue to violet with fuscous borders of various width; forewings with elliptic, gray to black, androconial brands variously conjoined to the fuscous distal ground; hindwing with long tail at vein CuA2 terminus, short tail, vein CuA1 terminus. Under Surface of Wings: ground colors ranging from white to dull gray-brown

contrasting fuscous-edged bands of yellow, orange, brown or red—forewing with disjunct or continuous band extending from costa to inner margin, hindwing with medial band comprised of variously pronounced lunular and/or lineal elements usually angled in a W-shape toward the anal margin. Hindwing limbal area with bright yellow, orange, or reddish Thecla-spot bordered by various suffusive marks. Length of Forewing: 10.0–14.0 mm. *Female.* Upper Surface of Wings: similar to that of male but fuscous margins wider and forewings lacking brands. Under Surface of Wings: similar to that of males but often with wing bands more pronounced. Length of Forewing: 10.0–14.0 mm. *Male Tergal Morphology and Genitalia* (figs. 58, 72–74, 78–80). Tergite 8 unspecialized (lacking subcordate incised posterior cavity), terminal margin entire and edged with thin, elongate microtrichia. Dorsoterminal surface of genitalia with two small brush organs abutting lateral edge of vinculum; length of brushes not exceeding terminus of labides. Genitalia with lateral surface of vinculum more angled than in *Nesiostrymon,* saccus thin and elongately parabolic. Valvae diminutive, length not exceeding caudoventral diameter of vincular arc (fig. 57), valval ventrum uniplanar and mostly flat. Valvae termini occurring as two, centrally located caudal extensions (fig. 58) each terminating with elongate, proximally protruding, microtrichia; distad these, a lightly sclerotized extravalvular element. Bilobed areas of valvae (fig. 58) with bilaterally symmetrical patches of nearly transparent sclerotin, ventral valval shapes and lengths of caudal extensions varying greatly between species. Aedeagus length usually exceeding rest of genitalia by one-fourth to one-third, shaft generally straight, caecum comprising one-fourth to one-fifth aedeagal length. Terminus of aedeagus with two, spinelike, cornuti. *Female Tergal Morphology and Genitalia* (figs. 60–71, 75–77). Tergite 8 unspecialized but papillae anales heavily sclerotized and tapering steeply to a point. Genitalia with sclerotized cephalic and caudal ductal elements joined by a constricted, transparent neck; directed ventrally from transparent neck, a prominent sclerotized bulb (the "bulb," figs. 69–71, 75–77). Relative lengths and breadths of ductal elements and adjacent bulb differ greatly between the

species. Corpus bursae with two small, pronglike signa.

TYPE SPECIES: *Thecla tera* Hewitson (1863–1878 [1878]) by original designation.

DISTRIBUTION: Primarily mainland with five generally allopatric species replacing each other in ranges from central Mexico south through the Andes and Amazon headwaters to montane northern Argentina and southeastern Brazil; one species endemic to southern Hispaniola.

DISCUSSION: *Terra* species are grouped below according to the two nested sets of taxa apparent in the cladistic analysis—Antillean and mainland. Of the five members comprising the mainland set, three allopatric taxa (*T. tera, T. andevaga, T. cana*) exhibit lunulate yellow to orange under surface bands and are referred to as the "yellow-banded species." Wing patterns in these species differ mostly in the shape and extent of bands and occurrence of adjacent yellow or orange pattern elements in the discal area. Of the yellow-banded members, *T. tera* is the most widely distributed, reminiscent of *N. celona* in *Nesiostrymon.* Other yellow-banded members are regionally isolated. Wing patterns of remaining mainland congeners (*T. chilica, T. calchinia*) exhibit bold brown or red bands with numerous additional pattern elements in the adjacent basal or distal areas. These latter taxa are grouped below as the "red- or brown-banded species."

It is important to note for diagnostic purposes that color and pattern differences in *Terra* taxa, though striking in actual specimens, become less evident in black and white photographs. Lightly colored under surfaces (white in some *Terra* species) require a fast shutter speed favoring pattern detail over ground contrast. As a result, photographs of some under surface patterns (the photos with darker backgrounds, figs. 33–56) appear more uniform than the actual specimens and vivid contrasts between brown and blue upper surface colors and white wing fringes are not always apparent (figs. 53, 55). In addition, pattern (but not color) similarities occur between species of *Terra* and some outgroup taxa. Confusing instances are pointed out in Discussion sections of appropriate species entries.

Cladistic analysis indicates little structural homogeneity among the wing pattern groups
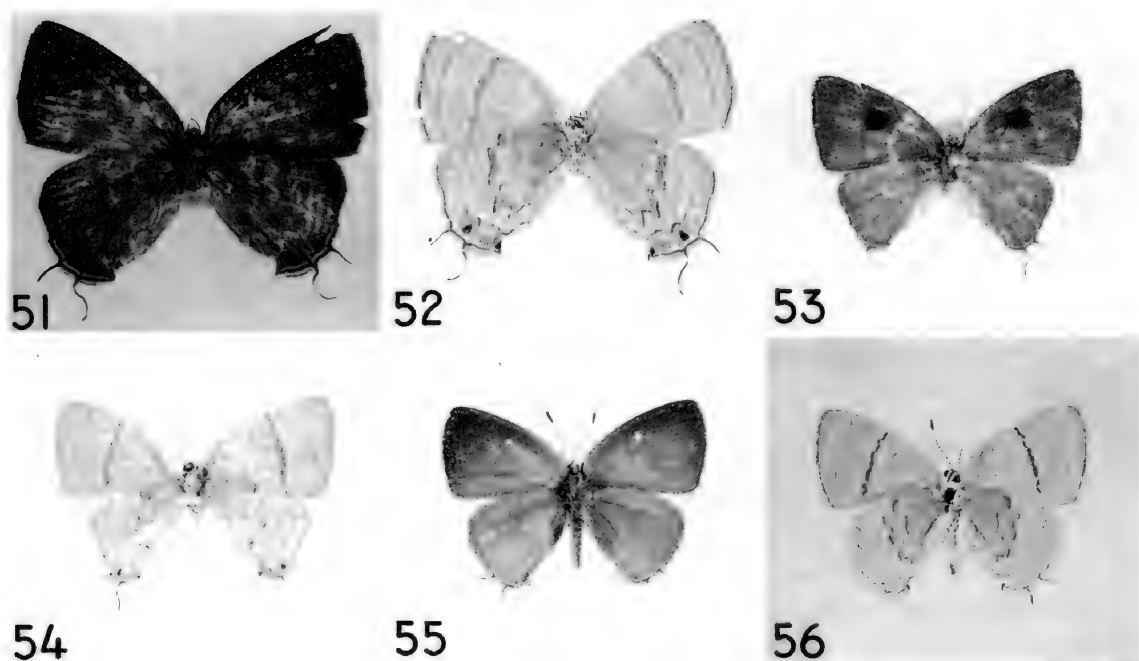
Figs. 51–56. Adults of *Terra*. *T. calchinia*: **51, 52.** Upper surface, under surface, female, "Amazon" (HEC). *T. chilica*: **53, 54.** Upper surface, under surface, male, Rolandia, Brazil (AMNH); **55, 56.** Upper surface, under surface, female, same data (AMNH).

comprising *Terra*. For instance, red-banded *T. calchinia* has a square-shaped valvae like that in yellow-banded *T. tera* but brown-banded *T. chilica* exhibits parabolic valvae like that in yellow-banded species *T. cana* and *T. hispaniola*. Remarkably, one yellow-banded species (*T. hispaniola*) stands out structurally in the cladistic analysis. Such heterogeneity results in my treating *Terra* as six species. Johnson and Matusik (1988) included a sixth taxon (*Thecla hyccara* Hewitson) in a list of probable *Terra* species. The female of *T. hyccara* was unknown at the time; subsequent inclusion of male and female characters in the cladistic analysis (fig. 85) indicated *T. hyccara* belonged to another, mostly undescribed generic level outgroup of *Nesiostrymon* and *Terra* (fig. 85).

ANTILLEAN TAXA

Terra hispaniola Johnson and Matusik
Figures 33–36, 69, 72

Terra hispaniola Johnson and Matusik, 1988: 241. — Schwartz, 1989: 241.

DIAGNOSIS: Superficially similar to yellow-banded mainland congeners reviewed below. From these, differing by wings' duller upper surface lavender color and under surface obsolescent bands in which lack of an outstanding medial mark in cell RS causes the band to appear basally directed from vein M2 to costa. Female genitalia robust, caudal ductal element uniquely larger than cephalic element with ventral bulb thickly conjoined to latter element. Male genitalia more typical of genus but with diminutive, elliptical valvae terminating with a slightly recurvate caudal extension.

DESCRIPTION: *Male*. Upper Surface of Wings: ground color dull violet blue, margins and apices suffused black; forewing with outstanding elliptical brand; hindwing with long tail at vein CuA2 terminus, short tail at vein CuA1 terminus. Under Surface of Wings: ground color, gray-white, forewing with gray-suffused postmedial line, costa to cell CuA1; hindwing with medial band of discontinuous yellow or yellow-gray patches, darkly suffused at edges, with no outstanding medial mark in cell RS causing band to appear basally directed from vein M2 to costa; limbal

area with light yellow Thecla spot centered with a black dot. Length of Forewing: 11.0–13.0 mm. *Female.* Upper surface of Wings: similar to that of male but fuscous marginal areas wider and forewings without brands. Under Surface of Wings: similar to that of males. Length of Forewing: 12.5 mm (allotype). *Male Tergal Morphology and Genitalia* (fig. 72). Tergite 8, brush organs, and genital vinculum, saccus, and aedeagus typical of genus. Valvae diminutive, elliptical in bilobed area, tapered terminally to slightly recurvate caudal extensions. *Female Tergal Morphology and Genitalia* (fig. 69). Tergite 8 and papillae anales typical of genus. Genitalia with length of cephalic ductal element nearly twice that of caudal element and with both elements very robust (cephalic element length only 6–7 times width compared to 15–21 times length incongeners). Bulb located rather flush with terminus of cephalic ductal element, not on semidetached stalk typical of congeners.

TYPES: Holotype male, allotype female, CMNH. Type Locality: "Middle Abejas" [sensu Johnson and Matusik, 1988], Las Abejas, Pedernales Province, Dominican Republic, July 6, 1986, leg. K. Johnson (genitalic dissection "AMNH/HS #106, 107," transferred to CMNH).

DISTRIBUTION (fig. 82): Known only from the Las Abejas rain forest in the Sierra de Baoruco of the Dominican Republic (southern paleoisland).

DISCUSSION: The original description did not mention the basal displacement of the under surface hindwing spot in cell M1. This character became apparent in studying this species in a revisionary context and examining additional specimens. It is also apparent from recent collections (figs. 33, 34) that yellow banding can be very reduced on some specimens. Because these specimens resemble *Nesiostrymon celida,* we suspect *T. hispaniola* may have been collected by early workers and misidentified as *"Thecla" celida.* As a result, curators should carefully examine series of *N. celida* for possible specimens of *T. hispaniola.*

Johnson and Matusik (1988) commented first on the field ecology of *T. hispaniola.* Its occurrence is limited to mesic broadleaf deciduous forest, where it inhabits areas more upland and xeric than *N. celida. T. hispaniola* is more vagile than *N. celida.* At Las Abejas, in contrast to the perching habits of *N. celida* (see its entry and Biogeography), *T. hispaniola* is a limited patroller, ranging from areas of broken canopy at 1190–1200 m altitude to the margin with pine forest at 1250 m altitude. To date, *T. hispaniola* is known from nine males and one female. Such disparity of males and females parallels that seen in series of *T. cana,* the only other *Terra* species recently collected in numbers. These circumstances may indicate females of *Terra* species are more habitat specific than patrolling males. Herein, along with the allotype female of *T. hispaniola* (figs. 33, 34), I illustrate a recently caught male with reduced under surface bands (figs. 35, 36).

MATERIAL EXAMINED: In addition to types listed above—DOMINICAN REPUBLIC. Same locality as primary types, July 5, 1984, leg. D. Matusik (1♂) (AMNH/HS 108 transferred to DMC) (DMC), July 30, 1990 (1♂) (AMNH, figs. 35, 36), (1♂) (AME), 1♂ (DMC); "Upper Abejas" (sensu Johnson and Matusik, 1988), patrolling path, July 13, 1987, leg. K. Johnson, on lifetime loan to Albert Schwartz (1♂) (AMNH/HS 109 transferred to AME) (AME); same location as primary types, nectaring on small blue flowers in sunlight, July 15, 1987, leg. K. Johnson (1♂) (AMNH/HS 110) (AMNH); "Upper Abejas," June 29, 1988, leg. D. Matusik (1♂) (DMC), June 30, 1988, leg. K. Johnson (1♂) (AME).

MAINLAND TAXA

As previously noted, structurally heterogeneous mainland taxa are divisible into two groups based on color of the under surface bands. Since yellow-banded species are most similar to *T. hispaniola,* they are treated first.

Yellow-banded Species

Terra tera (Hewitson)
Figures 37–40, 70–73

Thecla tera Hewitson, 1863–1878 [1878, vol. 1]: 211; [1878, vol. 2]: pl. 84, figs. 714, 715. — Godman and Salvin, 1879–1901 [1887, vol. 2]: 86. — Hoffman, 1940: 717. — Comstock and Huntington, 1958–1964 [1964]: 124. — Clench,
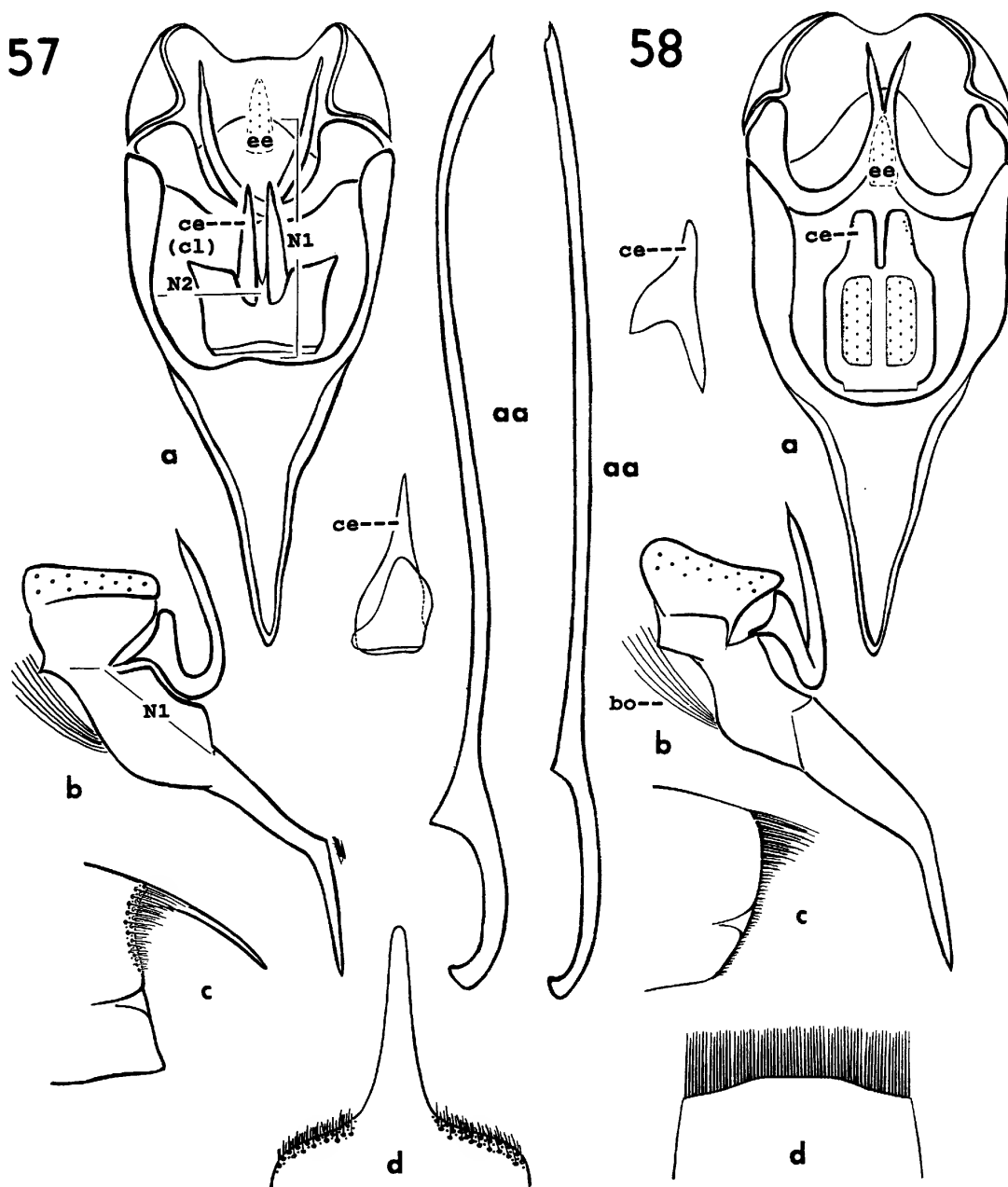
Figs. 57, 58. Generalized male genital and tergal structures of *Nesiostrymon* (57) and *Terra* (58). **a.** ventral view, genitalia with aedeagus removed and placed along side (aa); **b.** lateral view, genitalia; **c.** lateral view, terminal tergite and microtrichia; **d.** dorsal view, terminal tergite and microtrichia. ce, caudal extension of valvae (= cl, central lobe, in *Nesiostrymon*); ee, extravalvular element; bo, brush organs; N1, caudoventral diameter of vincular arc; N2, radius of vincular arc; stipples, areas of relatively transparent sclerotization.

1964: 251. — Ross, 1976: 198. — Bridges, 1988: I.344, II.77.
Terra tera: Johnson and Matusik, 1988: 235 (as type species).

DIAGNOSIS: Differing from other yellow-banded mainland species (*T. cana, T. andevaga*) by (i) upper surface iridescence dull blue with fuscous borders comparatively nar-
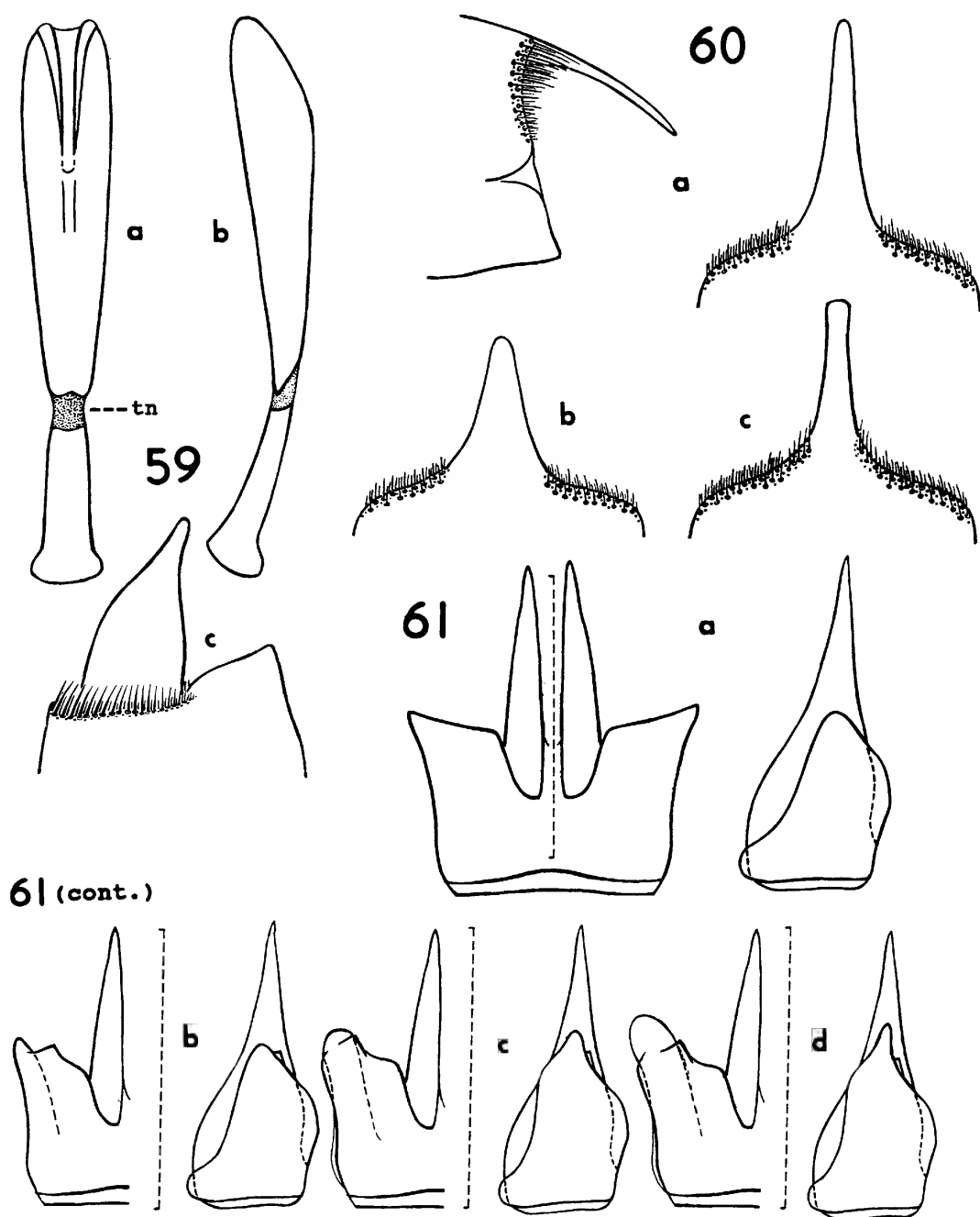
Figs. 59–61. Morphology of *Nesiostrymon celida*. **59.** Female. Genitalia. **a.** ventral; **b.** lateral; **c.** terminal tergite, papillae anales, and microtrichia. **60, 61.** Male. Terminal tergite in *N. celida* subspecies. (60). **a.** nominate, lateral view (left), dorsal view (right); **b.** *N. c. baocucoensis,* dorsal; **c.** *N. c. aibonito,* dorsal. Valvae in *N. celida* subspecies. (61). **a.** nominate, ventral (both lobes, with midline dashed) (left), lateral (right); **b.** *N. c. aibonito,* Puerto Rico, ventral (left of midline only) (left), lateral (right); **c.** *N. c. aibonito,* Hispaniola, same views; **d.** *N. c. baorucoensis,* same views. tn, transparent neck; stipples, areas of relatively transparent sclerotization.

row (others with wide apical, subapical, or submarginal fuscous borders), (ii) under surface medial band generally continuous from cell M1 to anal margin with adjacent discal streak obsolescent or absent. Male genitalia with valval base robust and square-shaped, caudal extensions (comprising up to one-third valval length) prominent compared to congeners; female genitalia with ductal elements most robust of mainland taxa, length of cephalic element exceeding that of caudal element by only about one-half (former greatly elongate in *T. andevaga* and the red- and brown-banded species).

DESCRIPTION: *Male*. Upper Surface of Wings: ground color dull iridescent blue with thin black marginal and apical borders. Forewing with postmedial elliptic gray brand surrounded by iridescent blue. Hindwing with long tail at vein CuA2 terminus, short tail at vein CuA1 terminus. Under Surface of Wings: ground color chalky white; forewing with thin yellow-orange postmedial line, narrowly bordered with black and sometimes with adjacent gray discal slash; hindwing with generally continuous medial band of elongate yellow-orange patches bordered distally with black. Discal area sometimes with light gray or obsolescent slash; outer marginal line with dull crenate markings; limbal area with prominent yellow Thecla spot centered with black dot. Length of Forewing: 11.0–13.0 mm. *Female*. Upper Surface of Wings: similar to that of male but with fuscous margins wider and forewing without brands. Under Surface of Wings: similar to that of male. Length of Forewing: 11.0–13.0 mm. *Male Tergal Morphology and Genitalia* (fig. 57, 73). Tergite 8, brush organs, genital vinculum, and saccus typical of the genus. Valvae ventrum robust with square base and prominent caudal extensions comprising up to one-third entire valval length. Aedeagus shaft bowed, caecum comprising about one-fourth aedeagal length. *Female Tergal Morphology and Genitalia* (fig. 70). Tergite 8 and papillae anales typical of genus. Genitalia with ductal elements robust compared to mainland congeners: caudal element length about one-half that of cephalic element; cephalic element thin (diameter about one-half that of caudal element) but not greatly elongate as in *T. andevaga, T. calchinia,* and *T. chilica.* Lamellae of caudal

element diminutive lamellae; cephalic element flared widely and with slight dorsal inclination. Bulb robust and elliptical, length comprising about one-fifth length of caudal ductal element.

TYPES: Holotype male, ZMH, labeled "Origin," "Thecla tera Hew.," "Coll. Stgr.," "Zool. Mus. Berlin" (Johnson and Matusik, 1988: 242 was an inadvertent listing error). Type Locality: original description lists Chiriquí, Panama.

DISTRIBUTION (fig. 82): Known from Veracruz State, Mexico, southward to the Cauca Valley of Colombia.

DISCUSSION: In an index, Bridges (1988) included *tera* under *Nesiostrymon,* based probably on Clench's (1964) remarks. Consistent with my taxonomic discussion under the generic entry, and because Bridges did not use formal binomials, I do not include his index citation in the synonymy. Ross (1976) noted the habitat of *T. tera* occurring in the Sierra de Tuxla of Yucatan, Mexico, as "Lower Montane Rain Forest" characterized by a *Terminalia-Dalbergia* association at 50–3000 m. This habitat was noted as drier than upland "Montane Forest or Cloud Forest." This xeric affinity of *Terra* is consistent with our observations of *Nesiostrymon celida* and *Terra hispaniola* in the Antilles (see Biogeography) but does not appear true of *T. andevaga* (noted herein from "submacrothermic rain forest") and *T. cana* (label data indicating "mesic to hydric forest"). Thus, some habitat segregation may be active in certain *Terra* taxa (see *T. andevaga* Discussion).

MATERIAL EXAMINED: In addition to type listed above—COLOMBIA. Rio Sucio (1♀) (BMNH); Q. Tasajera, 1300 m, February 19, 1949 (1♂) (AMNH). COSTA RICA. Irazú, 6–7000 ft (2♂, 1♀) (BMNH); Costa Rica (1♂) (BMNH). MEXICO. Catemaco, Vera Cruz, September 1957, leg. Escalante (1♂) (AME); Chiapas, no other data (3♂), September 1955 (1♂), September 1949 (1♂), August 1942 (1♂) (all AME); Jalapa, 4600 ft, November 1912, leg. A. Hall (2♀) (AME); Presidio, Vera Cruz, December 1935, leg. Escalante (1♂), May 1945, leg. Escalante (1♀), May 1948, leg. Escalante (1♂), April 1942, leg. Escalante (1♂) (all AME); San Lui Potosi, May 1973, leg. H. A. Freeman (1♂) (AME), June 2, 1973, leg.

Freeman (1♂) (both AME); Santa Rosa Comitan, May 1960, leg. Escalante (1♂) (AME). GUATEMALA. S. Geronimo, leg. Champion (1♀) (BMNH). NICARAGUA. Jinotaga, November 1905, wet season, 3400 ft (1♂) (BMNH). PANAMA. Chiriquí, 2500–4000 ft, leg. Champion (1♀) (BMNH). GUYANA. Mt. Roraima, leg. H. Whitely (1♂) (BMNH). VENEZUELA. Miranda, D.F., Rio Chacaito, 950 m, February 15, 1936, leg. Lichy (1♂) (AME); Metotan, September 2, 1937 (1♂) (AME).

Terra andevaga, new species
Figures 41–44, 71, 74

DIAGNOSIS: Distinctive in large size and broad wing expanse (FW to 14.0 mm) with broad upper surface black borders and adjacent forewing brands widely separated by iridescent blue ground color. On under surface, medial yellow patches more pronounced than in *T. tera* or *T. cana* and greatly disjunct. Male genitalia with base of valvae very small, square, and terminating with thickly tapered caudal extensions comprising about three-eights of the valval length; female genitalia with cephalic ductal element greatly elongate, nearly twice length of caudal element.

DESCRIPTION: *Male.* Upper Surface of Wings: ground color dull light iridescent blue with wide, black, subapical and submarginal forewing borders; pronounced elliptic postmedial forewing brands bordered distally by iridescent blue for at least 1.5 mm basad of fuscous wing borders. Hindwing with long tail at vein CuA2 terminus, short tail at vein CuA1 terminus. Under Surface of Wings: ground color chalky white, forewing with prominent bipartate yellow-gray postmedial band and discal slash; hindwing with pronounced yellow to yellow-orange patches forming disjunct medial band and prominent discal slash. Outer margin bordered with pronounced yellow-gray crescents; limbal area with large yellow-orange Thecla spot centered with a prominent black spot. Length of Forewing: 13.0–14.0 mm. *Female.* Upper Surface of Wings: similar to that of males but with fuscous marginal areas much more extensive, blackening all areas distad of fore-

wing discal cell. Under Surface of Wings: as on males. Length of Forewing: 13.0 mm–14.0 mm. *Male Tergal Morphology and Genitalia* (fig. 74). Tergite 8, brush organs and genital vinculum, saccus, and aedeagus typical of genus. Valvae ventrally diminutive with square base and prominent, thickly tapered, caudal extensions comprising about two-fifths overall valval length. Aedeagus elongate as typical of genus, shaft bowed, caecum comprising no more than one-fifth aedeagal length. *Female Tergal Morphology and Genitalia* (fig. 71). Tergite 8 typical of genus. Papillae anales less evenly tapered toward terminus, and more terminally declined than congeners. Genitalia with elongate, thin, cephalic ductal element similar to that of *T. calchinia* and *T. chilica* but much longer, nearly twice length of caudal ductal element. Bulb elliptical and robust, length equaling about one-fourth that of caudal ductal element.

TYPES: Holotype male, allotype female, Santo Domingo de los Colorados, Pichincha, Ecuador, "submacrothermic rain forest," December 24, 1969, leg. H. Descimon, deposited AMNH. Paratypes. AMNH: same data as primary types (one male); BMNH: Cashaurcu [Casahuaycu?], E. Ecuador, 4000 ft, leg. Palmer (one female); MNHN: "Equateur" (1♂).

DISTRIBUTION (fig. 82): Known from upland submacrothermic rain forest in Ecuador.

DISCUSSION: Though poorly represented in collections, this species has been collected in series as recently as 1969. In contrast to regionally sympatric *N. celona, T. andevaga* appears distinct from *T. tera* of the Colombian Cordillera. Along with the structural characters, the widely disjunct forewing androconial brand and under surface bands appear to be stable characters, occurring on an apparent dwarf specimen (10.0 mm) as well as on the large specimens characterizing the types. Johnson (1989e) noted range disjunction dividing thecline species of the genus *Orcya* into respective distributions in the Colombian Cordillera and nuclear Ecuadorian highlands. Certain insular species were restricted to upland cloud forest while wideranging xerophiles were conspecific throughout the northern Neotropical region. From the known habitat data, it appears *T. andeva-*
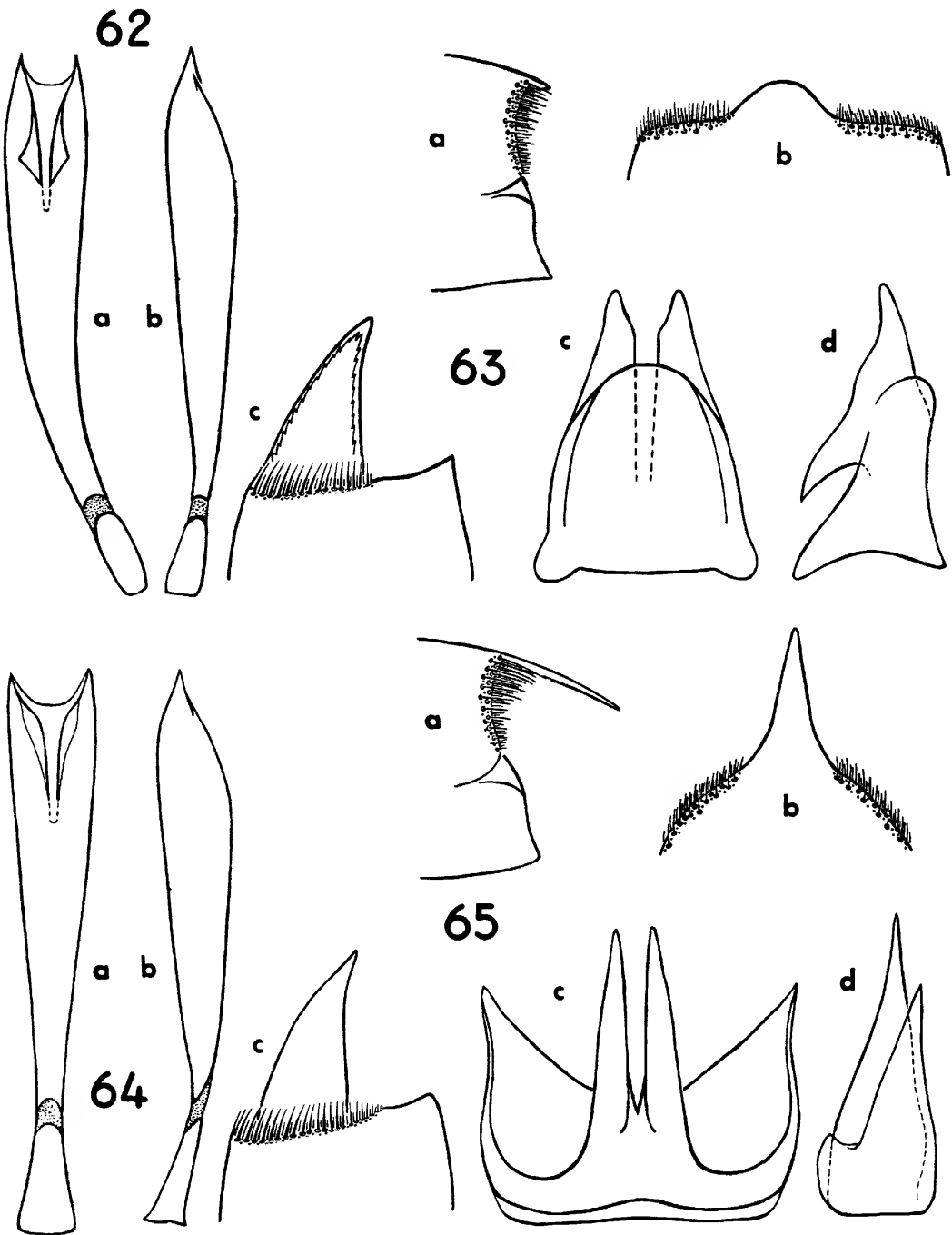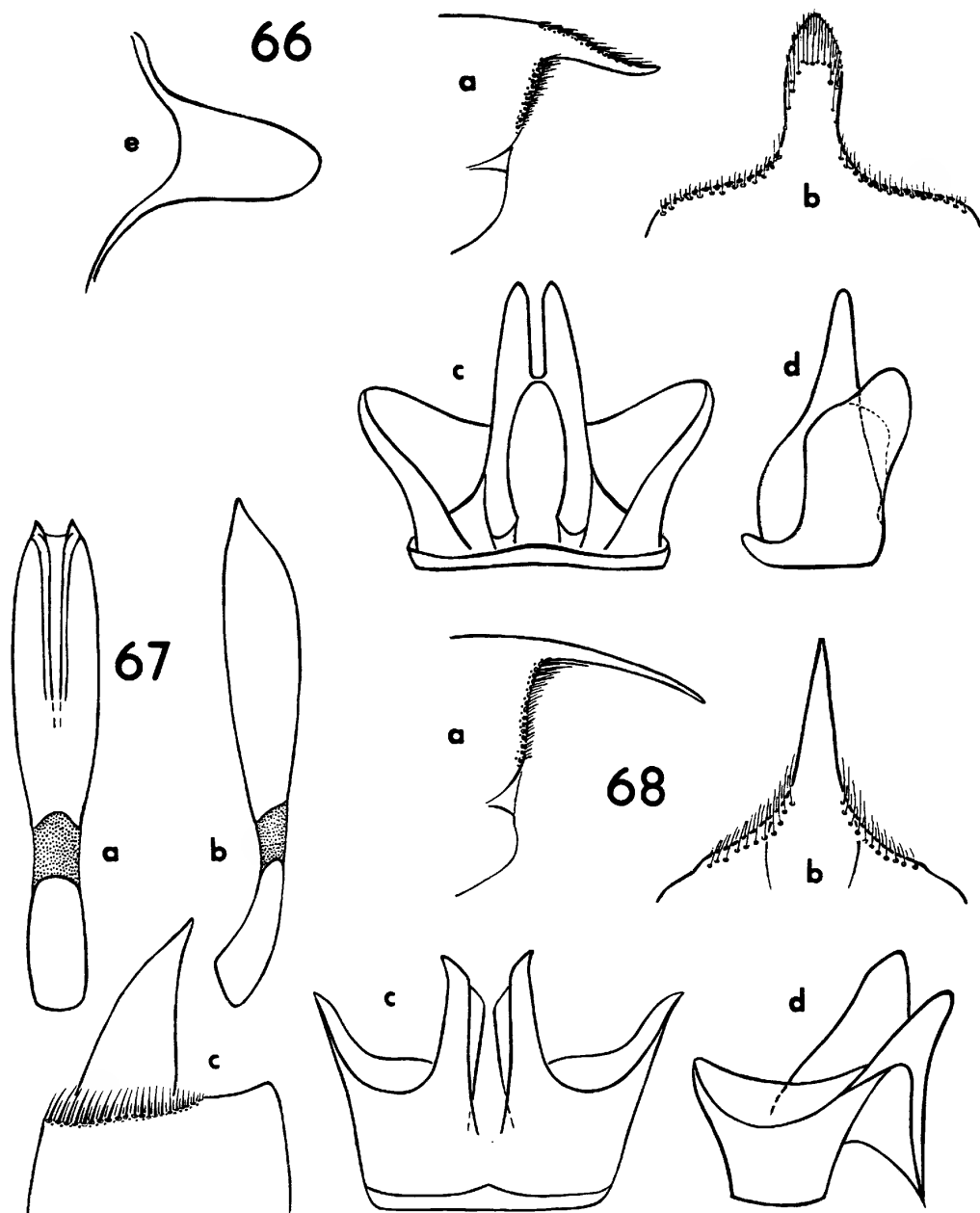
Figs. 62–65. Morphology of *Nesiostrymon shoumatoffi* and *N. celona*. *N. shoumatoffi*: **62.** Female. Genitalia (format as in 59). **63.** Male. Terminal tergite. **a.** lateral; **b.** dorsal; valvae; **c.** ventral; **d.** lateral. *N. celona*: **64.** Female (format as in 62); **65.** Male (format as in 63). Stipples, areas of relatively transparent sclerotization.

ga may be restricted to upland Ecuadorian cloud forest while *N. celona* ranges widely throughout the region.

MATERIAL EXAMINED: In addition to types listed above—ECUADOR. Balzapamba, Prov. de Bolivar, 1893–1894, leg. de Mathan (1♂ [forewing 10.0 mm, construed as a dwarf, see Discussion above] (BMNH)).

Figs. 66–68. Morphology of *Nesiostrymon milleri* and *N. australivaga*. *N. milleri*: **66.** Male (format as in 63, except **e.** lateral view, unique vincular spur). *N. australivaga*: **67.** Female (format as in 59). **68.** Male (format as in 63). Stipples, areas of relatively transparent sclerotization.

Terra cana (Hayward), new combination
Figures 45–48, 75, 78

Thecla cana Hayward, 1949: 571, fig. 7. — Comstock and Huntington, 1958–1964 [1959]: 174. — Hayward, 1973: 155. — Bridges, 1988: I.68, II.105. — Johnson and Matusik, 1988: 235.

Thecla tera [not *tera* Hewitson, 1863–1878 (1878)]: Hayward, 1973: 158 (misidentification of *T. cana* females, see Discussion below).

DIAGNOSIS: Medial elements of hindwing under surface band generally disjunct (often appearing as arc of spots) and paralleled by

a prominent, orange-bordered discal slash or line from cell RS to cell CuA1; forewing upper surface with wide fuscous apices, obscuring identification of sexes by means of the androconial brand (see Discussion below). Male genitalia with wide-rimmed, elliptical valvae; female with laterally compressed ductal elements of about equal size, terminating with widely flared lamellae.

DESCRIPTION: *Male.* Upper Surface of Wings: ground color pale iridescent blue to lavender, margins and apices clouded fuscous; forewing with brand generally contiguous with subapical fuscous; hindwing with long tail at vein CuA2 terminus, short tail at vein CuA1 terminus. Under Surface of Wings: ground color chalky white; forewing with faint, discontinuous, yellow postmedial band; hindwing with faint, discontinuous, yellow medial band paralleling a postbasal line from cell RS to cell CuA1. Outer margin lined with faint yellow-gray crescents; limbal area with faint yellow Thecla spot. Length of Forewing: 11.0–12.5 mm. *Female.* Upper Surface of Wings: similar to that of male but with fuscous marginal borders wider and forewings without brands. Under Surface of Wings: similar to that of males. Length of Forewing: 11.0–12.5 mm. *Male Tergal Morphology and Genitalia* (fig. 78). Tergite 8, brush organs and genital vinculum, saccus, and aedeagus typical of genus. Valvae ventrally elliptic with thick lateral rims tapered to blunt caudal extensions (length of latter slightly less than narrowest breadth of indented valval base). Base of valvae indented laterally to form two, shorter basal lobes. Aedeagus bowed, caecum comprising about one-fourth aedeagal length. *Female Tergal Morphology and Genitalia* (fig. 75). Tergite 8 typical of genus. Papillae anales with lateral surface heavily sclerotized, forming a raised midline. Genitalia with caudal ductal element laterally compressed, lamellae with widely flared lateral flaps; cephalic ductal element about same length as caudal element, but half as wide and not dorsally inclined. Bulb rather ovate, length equaling only about one-ninth that of caudal ductal element.

TYPES: Holotype male, labeled "Holotipo, Thecla cana Hayw., holotipo male, K. J. Hayward Det., preparacion genitalia male 4007, Villa Nougues, I 1931" deposited IML. Type

Locality: Villa Nougues, Tucumán Province, Argentina.

DISTRIBUTION (fig. 82): Known only from mesic woodland localities in Tucumán and Jujuy provinces of northwestern Argentina.

DISCUSSION: Hayward (1973) reported both *Thecla tera* and *T. cana* from Tucumán and did not closely associate the species. In his 1949 description of the latter species he did not mention *T. tera* and *T. cana* as similar. This seemed odd until Hayward's IML material was examined: a series identified as males and females of *T. cana* was, in fact, all males; a series identified as males and females of "*T. tera*" was, in fact, all females of *T. cana*. These misidentifications are attributable to the wide fuscous forewing apices of *T. cana* noted in the above Diagnosis. Even noting this distinction, I have confused the sexes of this species without dissection. Hayward's small series was mostly in very poor condition. An exception is the female illustrated in figures 43–44. Recently, R. Eisele and B. MacPherson have collected large numbers of *T. cana* in mesic to hydric forest areas of Jujuy and Tucumán provinces (see locality descriptions 5A in Johnson et al., 1988; 153A, 160B,C in Johnson et al., 1990). The disparity of sexes in recent samples of *T. cana* parallels our experience with *T. hispaniola* in the Dominican Republic. As heretofore noted, the wetter habitat indicated for *T. cana* parallels that reported for *T. andevaga* in Ecuador but contrasts that generally attributed to *T. tera* in Mexico and Antillean *T. hispaniola.*

MATERIAL EXAMINED: In addition to types listed above—ARGENTINA. "Tucumán," leg. Steinbach (1♂, 1♀) (BMNH); "Tucumán," 1100 m, January–February 1905, leg. Steinbach (1♀) (BMNH); "Tucumán," May 31, 1922 (1♀) (BMNH); Villa Nougues, Tucumán Province, January 21, 1931, leg. K. J. Hayward (1♂, 3♀), January 1929 (1♀) (IML); Quebrada de Lules, Tucumán Province, January 1929, leg. R. A. (1♂) (IML); Tucumán Province, Dept. Tafi Viejo, Las Pitas, 6 km N "El Portezuelo," Rte. 340, 1150 m, Rio Raco watershed, W slope Cumbre de Taficillo, January 19, 1987, leg. R. Eisele (1♂, 1♀) (AMNH); Tucumán Province, Dept. Yerba Buena, Yerba Buena ("El Paraiso") to Anta Muerta, Cumbres de Javier, Rte. 338, km posts 15 to

18, 700–900 m, December 31, 1987, leg. R. Eisele (AMNH) (22♂, 1♀); Jujuy Province, Cucho, south slopes Cerro Labrada, 1200–1500 m, January 11–16, 1987, leg. B. MacPherson (3♂, 2♀).

Red- and Brown-banded Species
Terra calchinia (Hewitson),
new combination
Figures 49–52, 76, 79

Thecla calchinia Hewitson, 1868: 21. — Kirby, 1871: 393. — Druce, 1907: 600. — Comstock and Huntington, 1958–1964 [1959]: 172. — Bridges, 1988: I.66, II.105. — Johnson and Matusik, 1988: 235.

DIAGNOSIS: Medial under surface bands prominently red-orange over white ground color, a pattern similar only to that of *T. chilica* which has prominent yellow-brown forewing band but a dappled hindwing pattern and distally angled wings. On *T. calchinia* the red-orange hindwing band is distinctly lunular adjacent vein RS and there is brilliant orange along the anal margin between the band and anal lobe. Male genitalia have square to hexagonal bases (much like those of *T. tera*) with short lobate caudal extensions; female genitalia exhibit an elongate cephalic ductal element as in *T. chilica* and *T. andevaga* but, compared to these, *T. calchinia* is much more robust (see below).

DESCRIPTION: *Male.* Upper Surface of Wings: ground color dull iridescent blue on basal two-thirds of forewing and across entire hindwing except submargins, distal borders of both wings fuscous. Forewing with large elliptical brand slightly darker than fuscous distal ground color. Hindwing with long tail at vein CuA2 terminus, short tail at vein CuA1 terminus. Under Surface of Wings: ground color bright gray-white; forewing with prominent tripartite band, deep red-orange centrally bordered on both sides by black and white; submargins with blackish-brown slashes in each cell; hindwing with tripartite medial band disjunct, consisting of a large red-orange costal spot, a jagged continuous band from vein RS to a pronounced "W"-shaped angle near the anal margin, and enlarged orbicular spot at the discal cell terminus. Limbal area with brightly contrasted white ground color, bold red Thecla spot, and

orange suffusion along the anal lobe. Length of Forewing: 11.5–12.5 mm. *Female.* Upper Surface of Wings: ground color brown, slightly flushed with blue iridescence. Under Surface of Wings: similar to that of male but with bands wider and hued red-brown. Length of Forewing: 11.5–12.5 mm. *Male Tergal Morphology and Genitalia* (fig. 79). Tergite 8, brush organs and genital vinculum, saccus, and aedeagus typical of genus. Valvae with wide distal rims and, depending on degree of slope along cephalic margin, squarish to hexagonal in shape with gradually tapered, lobate caudal extensions. Aedeagus with shaft quite straight, caecum comprising about one-fourth aedeagal length. *Female Tergal Morphology and Genitalia* (fig. 76). Tergite 8 typical of genus. Papillae anales distinctively lobate, with rather square termini differing from the steeply pointed structures of congeners. Genitalia similar to those of *T. chilica* and *T. andevaga* with relatively elongate cephalic ductal element. Of these, however, *T. calchinia* is most robust with latter element exceeding length of caudal element by about 1.3. Bulb relatively small, length comprising about one-eighth that of caudal ductal element.

TYPES: Holotype, male, BMNH, labeled "Thecla calchinia Hew. Type. Godman-Salvin Coll. 1912023., Ega, U. Amazons, H. W. Bates, B.M. Type. Rh 969." Type Locality: Ega, Upper Amazons, Brazil.

DISTRIBUTION (fig. 82): Known only from a few localities in the upper Amazon Basin of Amazonas State, Brazil.

DISCUSSION: This species is poorly represented in collections but very distinctive. It has received little report in the literature and label data suggest all of the specimens are old. Consequently, and because hairstreak identifications are uncertain at many museums, it is possible that additional specimens are to be found in old, unsorted materials. In black and white photos, the female under surface of *T. calchinia* somewhat resembles that of *Sipaea hycarra* (Hewitson). However, the latter species has brilliant blue on the hindwing upper surface and, on the under surface, brown bands over tawny ground color, not red bands over gray-white ground color as in *T. calchinia*.

MATERIAL EXAMINED: In addition to type listed above—BRAZIL. Ega, Upper Ama-
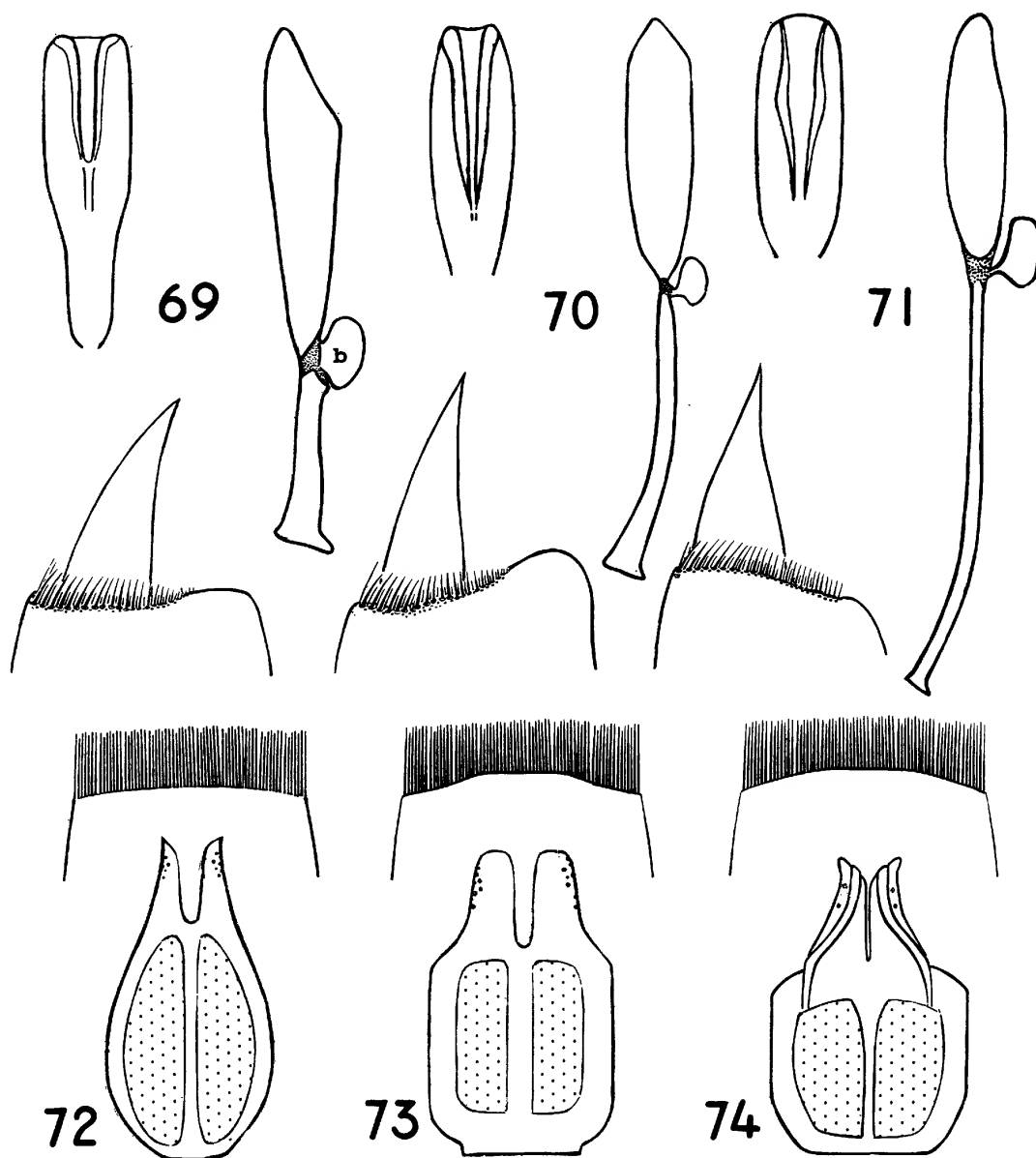
Figs. 69–74. Morphology of *Terra* species. *T. hispaniola*: **69.** Female. Genitalia, lateral (right), ventral caudad of bulb (b) (left, above). Terminal tergite, papillae anales, and microtrichia, lateral (below). **72.** Male. Terminal tergite and microtrichia, dorsal (above); valvae, ventral (below). *T. tera*: **70, 72.** (same views as for *T. hispaniola*). *T. andevaga*: **71, 74.** (same views as for *T. hispaniola*). b, bulb; stipples, areas of relatively transparent sclerotization.

zon, leg. Bates (1♂, 1♀) (BMNH); Tefé, Solimões, November 1919, leg. Parrish (1♂) (CMNH); Amazon, Bates, [18]35 (1♀) (HEC); São Paulo de Olivenca (1♂) (MNHN).

Terra chilica (Schaus), new combination
Figures 53–56, 77, 80

Thecla chilica Schaus, 1902: 422. — Comstock and Huntington, 1958–1964 [1959]: 184. —

Bridges, 1988: I.78, II.105. — Johnson and Matusik, 1988: 235.

DIAGNOSIS: Wing apices distally angled, forewing brand in males consequently appearing very large. Ground color of forewing (particularly in females) brown-hued, contrasting bright blue hindwing marked distally with vivid white fringe and tails. Under surface with wide yellow-brown medial band on
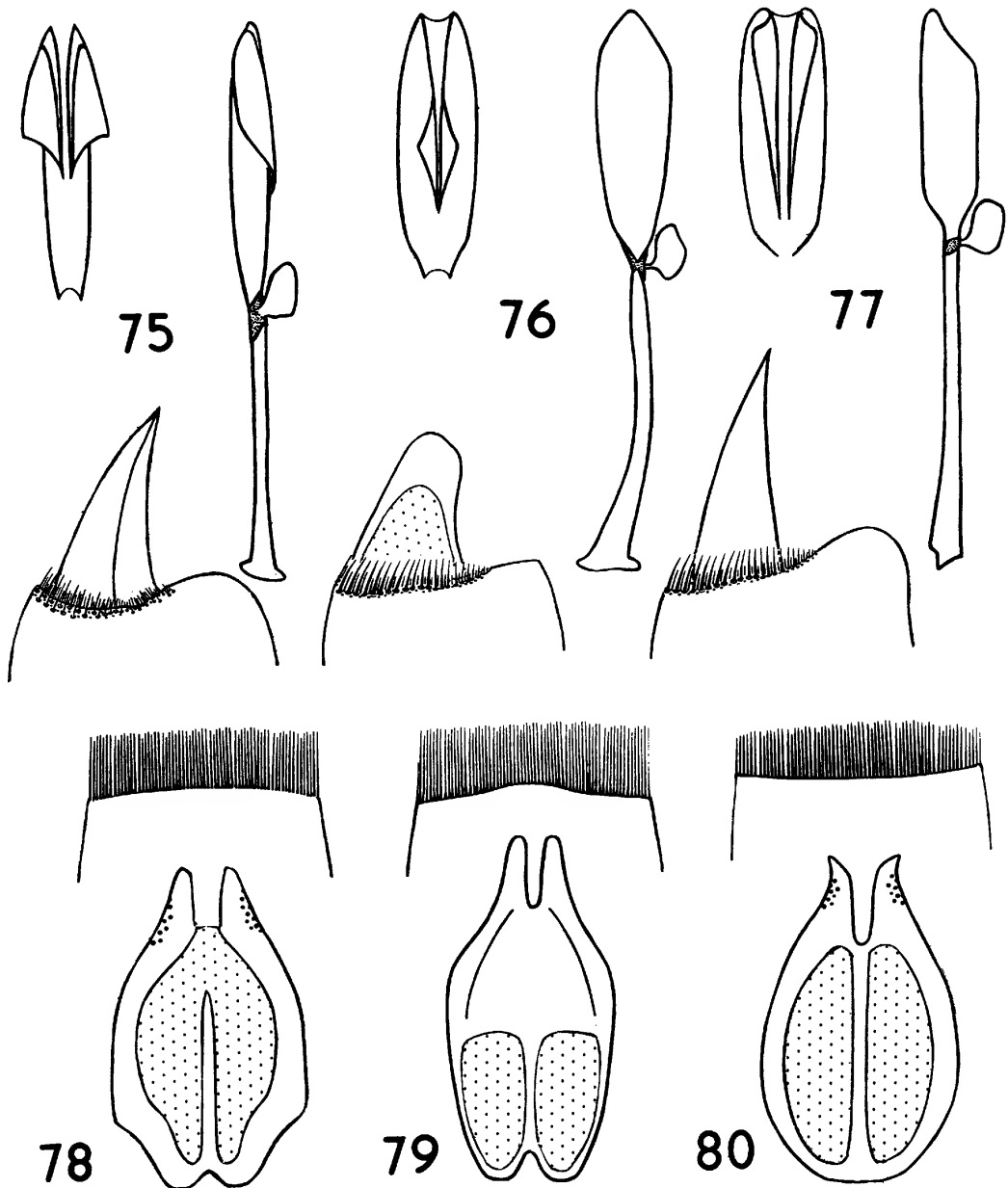
Figs. 75–80. Morphology of *Terra* species. Same views as figures 69–74. *T. cana*: **75, 78.** *T. calchinia*: **76, 79.** *T. chilica*: **77, 80.** Stipples, areas of relatively transparent sclerotization.

forewing, hindwing of dappled appearance from enlarged costal spot and variously disjunct discal and submarginal lines complementing the medial band. Male genitalia with valvae more prominent than in congeners (valve length only slightly less than caudoventral diameter of vincular arc) and base widely elliptical with extremely short caudal extensions; female genitalia with cephalic

ductal element elongate (though not extreme as in *T. andevaga*) with a short, robust caudal element.

DESCRIPTION: *Male*. Upper Surface of Wings: forewing ground color iridescent gray-blue, hued brown, with prominent gray brand closely adjacent fuscous apices and margins; hindwing ground color brighter blue with tails at vein CuA2 and vein CuA1 termini elon-

gate and, along with adjacent fringe, colored vivid white. Under Surface of Wings: ground color chalky white to gray; forewing with light gray submarginal line and prominent yellow-brown medial band; hindwing with lunular band of yellow to yellow-brown patches, costal element greatly enlarged and discal and submarginal areas more prominently marked with suffused elements than most congeners; limbal area with yellow-brown Thecla spot. Length of Forewing: 10.0–12.0 mm. *Female.* Upper Surface of Wings: ground color of forewing dull brown; hindwing markedly more blue with vivid white fringe. Under Surface of Wings: similar to that of males but sometimes with broader forewing band. Length of Forewing: 10.0–12.0 mm. *Male Tergal Morphology and Genitalia* (fig. 80a). Tergite 8, brush organs and genital vinculum, saccus, and aedeagus typical of genus. Valval more prominent than in congeners, widely elliptical with terminus tapering abruptly to two very diminutive caudal extensions (length comprising about one-sixth of total valvae length). Aedeagus elongate as typical of genus, shaft bowed, caecum comprising one-fourth to one-fifth aedeagal length. *Female Tergal Morphology and Genitalia* (fig. 77b). Tergite 8, in specimens examined, appearing more caudoventrally lobate than congeners. Papillae anales steeply pointed as typical of genus. Genitalia with cephalic element of ductus thin and elongate, length twice that of comparatively robust caudal element. Caudal element diameter three times that of cephalic element and ventroterminal opening thin, extending over terminal one-half of element and surrounded centrally by collarlike lips. Bulb rather rectangular, overlapping base of caudal ductal element and joined to transparent ductal neck by a short stalk.

TYPE: Holotype male, #5956, National Museum of Natural History (Smithsonian Institution). Type Locality: Castro, Paraná, Brazil.

DISTRIBUTION (fig. 82): Known from southeastern Brazil (Rio de Janeiro and Paraná states) west through southern Paraguay.

DISCUSSION: Like *T. calchinia,* this species has received little attention in the literature though every collection examined, with significant holdings from southwestern Brazil and Paraguay, contained a few specimens.

Some wing pattern variation is apparent in the samples: in southeastern Brazil, wing under surfaces are more dappled and the hindwing band quite lunulate; westward in Paraná State, Brazil, and in Paraguay, under surface ground colors are more concolorous and bands nearly linear (looking somewhat like those of *Nesiostrymon celona*).

MATERIAL EXAMINED: BRAZIL. Castro, Paraná, 2900 ft, Jones (2♂, 2♀) (BMNH); Iguassu, Paraná, December 30, 1921 (1♀), December 22, 1921 (1♂, 1♀) (BMNH); Palmar, Paraná, November 2, 1937 (1♀) (MPM); Rolandia, Paraná, December 1956 (2♀) (MPM); Rolandia, leg. Maller (1♀) (AMNH); Nova Teutonia, 1944 (1♀) (CMNH); Petropolis, 1939–1941 (1♀) (CMNH); Santa Barbara, October 12, 1926 (1♀) (MNHN). PARAGUAY. Villarrica, December 1923, F. Schade (1♀) (BMNH); Villarrica (1♂) (MPM), October 10, 1926 (1♂, 1♀) (MPM); Paraguay (4♂) (MNHN).

BIOGEOGRAPHY

HISTORICAL REVIEW

Clench (1964) erected *Nesiostrymon* as a monotypic genus for certain hairstreak butterflies he considered endemic to the Greater Antilles. He divided his type species, *N. celida,* into three interisland "subspecies": nominate (Cuba), *c. shoumatoffi* (Jamaica), and *c. aibonito* (Puerto Rico). At the time, these butterflies had seldom been collected and little was known of their habitats or actual distributions. No specimens had been reported from Hispaniola. Clench speculated that the hairstreak *Thecla tera* Hewitson, distributed from central Mexico to northern South America, might be a mainland "relative" of *Nesiostrymon.* Earlier, Draudt (1919) had grouped a number of taxa superficially similar to *N. celida* in his "*Thecla celida* Group": *T. celida, t. tera, T. celona* Hewitson, and *T. chilica* Schaus. Riley (1975) and Schwartz (1989) reported small numbers of *Nesiostrymon* from Hispaniola. Johnson and Matusik (1988) differentiated *Nesiostrymon* from *Terra* and described the sole Antillean member of *Terra.* In their work, Johnson and Matusik also made preliminary comments on the restricted local distributions and field ecology of *N. celida* and *T. hispaniola* in the

Fig. 81. Inset, map of Greater Antilles indicating geographic distribution of *Nesiostrymon*; below: map of Neotropical realm between 26°N and 40°S indicating geographic distribution of *Nesiostrymon*. Taxa Key: ◑ *N. celida celida*; ◑ *c. aibonito*; ○ *c. baorucoensis*; ◉ *N. shoumatoffi*; ● *N. celona*; ▲ *N. milleri*; ▼ *N. australivaga*.

Antilles. Although relatively few specimens of *N. celida* had been previously reported from the Antilles (Schwartz 1989), Johnson, Matusik, and members of a 1987 CMNH Hispaniolan expedition, secured large numbers after locating the microhabitat of the species.

Contrary to Clench's (1964) view, cladistic analysis indicates *Nesiostrymon* is not an endemic Antillean genus. Rather, *Nesiostrymon* and a sister lineage *Terra* both occur in the Antilles and on the mainland. *T. hispaniola* was discovered in habitat immediately adjacent to *Nesiostrymon* and, to date, has not been collected outside of the Las Abejas for-

est of the Dominican Republic (Schwartz, 1989). Miller and Miller (1989) listed a number of Antillean butterflies whose secretive habits and extreme microhabitat restriction make them improbable dispersers. As they note, documenting the local ecology of such species is germane to discussing their cladistic and distributional data.

LOCAL ECOLOGY OF
NESIOSTRYMON AND *TERRA*

On Hispaniola members of *Nesiostrymon* and *Terra* are sympatric in remote upland

mesic forests (Johnson and Matusik, 1988; Schwartz, 1989) of the southern paleoisland (Schwartz, 1989). *Nesiostrymon* has also been recorded from four localities on the northern paleoisland (Schwartz, 1989). In contrast to a few historical collection records, *N. celida* can be readily collected once its microhabitat is discovered. At "Las Abejas" (Sierra de Baoruco, Dominican Republic; see Johnson and Matusik, 1988) nearly a hundred specimens have been collected since 1981. The samples are mostly from early morning (9–1000 hr) in isolated enclaves of upland mesic deciduous forest (1100–1200 m) where *N. celida* occurs in damp ravine-bottom stands of *Gyrotaenia* [probably] *myriocarpa* (Urticaceae) (i.d. C. Whitefoord, Botany Department, BMNH). The microhabitat also supports other seldom-collected, locally restricted Hispaniolan endemics *Greta diaphana* (Drury) (Ithomiidae), *Anetia jaegeri* Ménétriés (Danaidae), *Battus zetides* Munroe (Papilionidae), and recently described *Leptotes idealus* Johnson and Matusik (Lycaenidae).

Local distribution of *N. celida* is very limited. Even in a supportive *Gyrotaenia* stand, the butterflies are not easily observed. If foliage is disturbed, a few individuals may be seen flying short distances of 5–10 m between shaded branches but, aside from this activity, adults remains mostly sedentary. Midday sun brings occasional individuals to nectar on flowers of adjacent clearings and paths. Because such individuals are more easily observed, I suspect most historical Antillean collections (including the small number reported by Schwartz, 1989) have occurred in this manner. Our early experience with the species was through such occasional sightings. We never collected *N. celida* in numbers until we located small stands of *Gyrotaenia* and sampled them in the early morning before many other butterflies were flying. *Gyrotaenia* is the primary perching substrate for *N. celida* at Las Abejas but since diverse vegetation is dense amid and around growths of *Gyrotaenia*, we have been unable to determine whether it is the larval foodplant. At Las Abejas, *N. celida* does not venture far from *Gyrotaenia* for nectar. The most common nectar source, *Palicourea barbinervia* (Rubiaceae) (i.d. E. de J. Marcano, MNDR) grows within a few feet of the *Gyrotaenia* stands we have sampled.

Terra hispaniola is still poorly known (nine males and one female at Las Abejas since 1985). Mainland species of *Terra* are also not common in collections. Published ecological notes mention *Terra tera* as "rare" in *Terminalia* L. (Combretaceae)–*Dalbergia* L. (Fabaceae) associations of "Lower Montane Rain Forest" (50 to 2500–3000 ft) in the Sierra de Tuxtla of Yucatan, Mexico, an association noted as more xeric than adjacent upland "Montane Forest or Cloud Forest" (2500–3000 to 5300 ft) (Ross, 1977). Xeric affinity of *Terra,* and mesic affinity of *N. celida,* is consistent with our observations of congeners in the Antilles. Las Abejas specimens of *T. hispaniola* have all been collected in areas of slightly broken canopy on narrow paths 50 m to 0.5 km upland from the mesic habitats of *N. celida.* At Las Abejas, *T. hispaniola* appears more vagile than *N. celida,* an individual seen in pine forest bordering the Las Abejas mesic forest at 1600 m altitude in 1987. As Schwartz (1989: 498–500) noted, *T. hispaniola* is one of several species of butterflies currently known only from Las Abejas. He speculated that if *T. hispaniola* and other Las Abejas endemics occur more widely on Hispaniola, they are probably restricted to the upland Sierra de Baoruco of the Dominican Republic and perhaps once occurred in the adjacent Massif de la Selle of Haiti before its deforestation. Of five endemic Lycaenidae described from Las Abejas (Johnson and Matusik, 1988), only *Strymon andrewi* has been collected more widely in the Sierra de Baoruco (Schwartz, 1989). Schwartz attributed this to the latter species being an upland pine forest xerophile while mesic deciduous forest biome characterizing the other species is rapidly being destroyed (Schwartz, 1989; Johnson and Matusik, 1988, In press; Johnson, 1989d).

CLADISTICS AND ANTILLEAN BIOGEOGRAPHY

With the advent of modern plate tectonic theory as a reference point, historical literature concerning biogeography of Antillean butterflies can be generally grouped in four categories: (1) pretectonic dispersalist explanations (Comstock and Huntington, 1949; Michener, 1943; Munroe, 1950; Clench, 1964; Miller, 1966, 1968); (2) posttectonic, primarily dispersalist, explanations (Scott,

Fig. 82. Map of Neotropical realm between 26°N and 40°S indicating geographic distribution of *Terra*. Taxa Key: ⊙ *T. hispaniola*; ● *T. tera*; ○ *T. andevaga*; ▲ *T. calchinia*; ■ *T. chilica*; ▼ *T. cana*.

1972, 1986; Brown and Heineman, 1972; Riley, 1975; Brown, 1978); (3) posttectonic vicariance-oriented reassessments without specific cladistic analyses (Shields and Dvorak, 1979; Buskirk, 1985; Miller and Miller, 1989); and (4) specific cladistic analyses relevant to establishing any general vicariant pattern among the butterflies (Ackery and Vane Wright, 1984; Shuey, 1986; Friedlander, 1986 [1987]; Johnson and Matusik, 1988).

Since the general acceptance of plate tectonic theory, concensus has developed among lepidopterists that both dispersal and some form of vicariance have contributed to present-day Antillean butterfly distributions. Miller and Miller (1989) summarized this

view and presented a combined vicariance/dispersal model for the evolution of the Antillean butterfly fauna. They present no cladistic data in their study but, based on a phylogenetic view of contemporary taxonomy and distributional data, discuss the plausibility of dispersal or vicariance explanations concerning Antillean butterflies and make numerous testable predictions.

Dispersal has undoubtedly affected the composition of the Antillean butterfly fauna. Historically, nearly all authors have characterized the Antillean butterfly fauna as "depauperate," composed of taxa with generally incoherent taxonomic relations to adjacent mainland groups. Indeed, ecological and distributional traits of much of the fauna do not

contradict an assessment of long-term random invasion coupled with subsequent climatic, eustatic, and ecological change influencing differential extinction (Fox, 1963; Scott, 1972, 1986; Brown and Heineman, 1972; Riley, 1975; Brown, 1978; Buskirk, 1985). Miller and Miller (1989) estimated roughly 60% of Antillean butterflies fit this profile. A smaller percentage of this number (5%, Scott, 1972) are well-documented long-distance dispersers. Biogeographers generally conclude that most Antillean butterfly taxa, like birds and mammals, are related to Middle American groups with less numerous, discordant elements, showing affinities to North and South America (Scott, 1972, 1986; Cruz, 1974; Riley, 1975; Bond, 1978, 1979; Brown, 1978; Olson, 1978; Buskirk, 1985; Miller and Miller, 1989).

Nonvagile elements have also always been recognized in the fauna and biogeographers have noted the importance of these sedentary elements in assessing the origin of the Antillean fauna (Fox, 1963; Brown, 1978; Scott, 1972; Riley, 1975; Buskirk, 1985; Johnson and Matusik, 1988; Miller and Miller, 1989). When the stable-Earth assumption dominated biogeography, early Caribbean workers explained sedentary Antillean endemics by land bridges (Fox, 1963) or an "ancient infusion" of farflung geographic elements by dispersal (Brown, 1978). Indeed, some authors invoked the small numbers of such nonvagile butterflies as a rationale for assuming discordant dispersal as the origin of most island faunas (Comstock and Huntington, 1949; Scott, 1972, 1986; Robbins and Small, 1981). In the Antilles, least vagile butterfly groups, like the ithomiids, polyommatines, primitive danaids, and certain endemic satyrids emphasized by Miller and Miller (1989) show limited occurrences, high endemism, and little taxonomic commonality among the islands. Included are members of *Leptotes* (Lycaenidae) and *Archimestra* (Nymphalidae) linked by most authors to ancient African antecedents, groups of species (like *Nesiostrymon* and *Terra*) known from restricted ecological niches, and certain endemic genera (like *Calisto,* Satyridae) exhibiting remarkable intraisland endemism. Miller and Miller (1989) provided detailed lists of these groups.

Most important to discussion in the present study is a group of elements recognized since the advent of plate tectonic theory— Antillean endemics with interisland distributions possibly concordant with hypothesized tectonic sequences (Shields and Dvorak, 1979; Shuey, 1986; Buskirk, 1985; Johnson and Matusik, 1988; Miller and Miller, 1989). Cladistic analyses of these groups are necessary to determine if a general pattern of vicariance is apparent among some Antillean butterflies.

VICARIANCE BIOGEOGRAPHY AND *NESIOSTRYMON* AND *TERRA*

Vicariance biogeography emphasizes areas of endemism as potential remnants of formerly continuous ancestral distributions and seeks to determine whether there are generalized, nonrandom, patterns in the affinities of endemic taxa correlating with information concerning geological history. Methods and applications of vicariance biogeography have been articulated in works by Platnick and Nelson (1978), Nelson and Platnick (1981), Wiley (1981), Rosen (1975), Patterson (1981) and Savage (1982).

Rosen (1975), using a tectonic scenario primarily derived from Malfait and Dinkelman (1972), proposed a seminal model for vicariance in the Caribbean region. Although this view was disputed (Pregill, 1981, and others), subsequent geological literature (Pindell and Dewey, 1982; Burke, 1988; Donnelly, 1988) generally supports the plausibility of a late Mesozoic-Tertiary tectonic origin for the Greater Antilles. Discussing the Neotropical herpetofauna, Savage (1982) summarized vicariance views of Antillean origins and enumerated predictions relevant to determining a general pattern. Miller and Miller (1989) refined these predictions with regard to Antillean Lepidoptera and, based on a tectonic scenario slightly modified from Pindell and Dewey (1982), proposed a vicariance model for the origin of several groups of Antillean butterflies. According to Miller and Miller, at least 5 clusters of butterfly genera suggest a late Mesozoic-Cretaceous vicariance pattern including Africa and the New World, 9 genera fit a late Cretaceous-Eocene vicariance of a "proto-Greater Antilles" from Central and South America, and some 20 intrageneric groups reflect post-Eocene breakup and

accretion among various tectonic elements of the Caribbean plate.

Cladistic analysis is basic to testing hypotheses of vicariance. Similar to the function of synapomorphies in character cladograms, vicariance biogeography construes congruence of unique areas of occurrence in area cladograms as evidence of a relationship. Generalized patterns of vicariance can only be established by studying many groups of organisms. However, study of particular groups provides the elements for these analyses. Congruences among area cladograms, if evidence of a general pattern, could result from either concordant dispersal or vicariance of an ancestral biota. Regarding Antillean butterfly origins, congruence in area cladograms is particularly relevant since biogeographers have debated whether the Greater Antilles have long remained in situ or whether they originated by eastward tectonic drift of ancient elements from the Central American region. If the former, Antillean biota must reflect over-water dispersal, a random phenomenon not open to objective scientific testing. If the latter, however, distributions of Antillean biota may be vicariant remnants of such movement and reflect a recognized tectonic pattern.

Two views of a vicariant origin are compatible with the area cladograms of *Nesiostrymon* and *terra*. The relative simplicity of these views appears compelling compared to a dispersal explanation requiring several coincidental and concordant over-water dispersals. Both views of vicariant origin require consideration since it is debatable whether *T. hispaniola* represents a northern Hispaniolan or southern Hispaniolan distributional element.

Historically, *T. hispaniola* may be a southern Hispaniolan element. Of five lycaenid species described by Johnson and Matusik (1988) and known to date only from the Sierra de Baoruco uplands (Schwartz, 1989), *T. hispaniola* and two [perhaps three] other species have immediate Jamaican affinities. The hairstreak *Heterosmaitia abeja* Johnson and Matusik is the sole known sister of Jamaican *H. bourkei* (Kaye). The polyommatine *Leptotes idealus* Johnson and Matusik shares its salient single hindwing eyespot and various structural characters only with upland Ja-

maican *L. perkinsae* (Kaye) (Johnson and Matusik, in press). A second hairstreak, *Electrostrymon minikyanos* Johnson and Matusik, may have a unique relation to *E. pan* (Drury) of Jamaica. However, because of the problem of polyphyly in current usages of *Electrostrymon*, affinities in the genus are uncertain (Johnson and Matusik, 1988; Johnson, 1991).

The view that *T. hispaniola* may be a northern Hispaniolan element stems from its local sympatry with *N. celida,* a species occurring on northern Hispaniola, Cuba, and Puerto Rico. Two factors, however, suggest that this sympatry results from dispersion of *N. celida* on Hispaniola. Firstly, another upland Sierra de Baoruco endemic (*Strymon andrewi* Johnson and Matusik) occurs on the north "rim" of the southern paleoisland and its sister taxon, *S. toussainti* (Comstock and Huntington), is pan-Hispaniolan. Secondly, the characters of Las Abejas *N. celida baorucoensis* are generally autapomorphic, not primitive.

Significantly, area cladograms of *Nesiostrymon* and *Terra* expressed as four taxon statements suggest late Cretaceous-Tertiary vicariance irrespective of the above interpretations concerning *T. hispaniola* (fig. 83). Using either interpretation, two features of *Nesiostrymon/Terra* area cladograms are consistent: (1) plesiotypy of the Jamaican/South Hispaniolan elements in both genera and (2) evidence of three taxon congruence.

Compatible with the Miller and Miller model, if *T. hispaniola* is considered a northern Hispaniolan element, proto-Antillean elements [PGA] and Jamaican elements [J] in *Nesiostrymon* and *Terra* vicariated in concert. This view requires only that the proto-Antillean element of *Nesiostrymon* maintain a strong ancestral range affinity to South American components [SA] of the genus, an observation compatible with Miller and Miller's view that the older the vicariance (e.g., Late Mesozoic-Cretaceous, p. 237–239) the stronger the affinity of proto-Greater Antilles to South America. The three-taxon congruence in this scenario is J/PGA + SA, Central America [CA]; PGA/SA + CA for *Nesiostrymon* and PGS/SA + CA for *Terra*. This scenario is also compatible with Miller and Miller's model when the proto-Greater Antilles

PALEOCENE

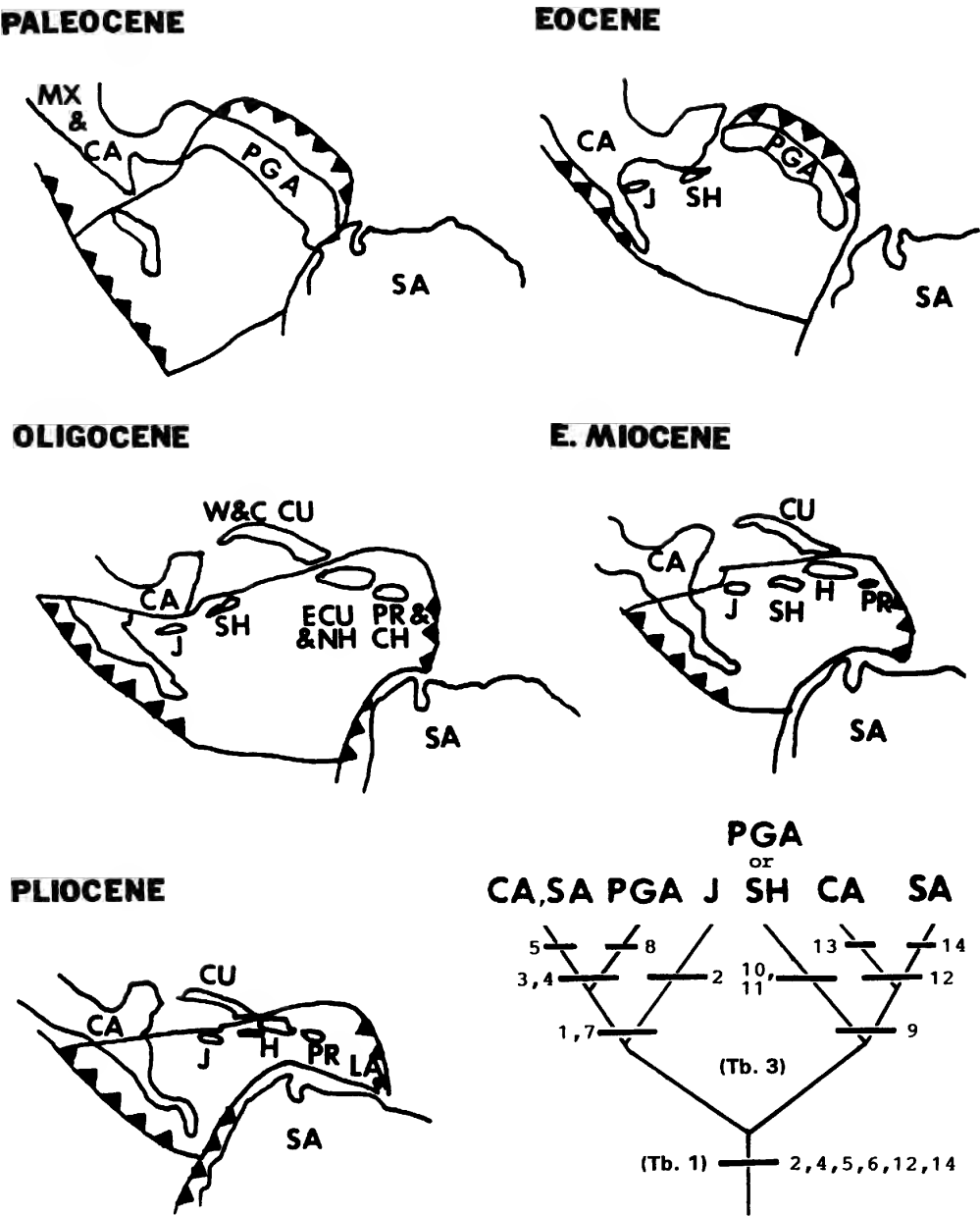**EOCENE**

OLIGOCENE

E. MIOCENE

PLIOCENE

Fig. 83. Paleocene to Pliocene tectonic scenario published in Miller and Miller's (1989) proposal of a vicariance model for Antillean Lepidoptera origins; below, right, area cladogram of *Nesiostrymon* and *Terra* species based on figure 2. MX, Mexico; CA, Central America; PGA, proto-Greater Antilles; SA, South America; J, Jamaica; SH, Southern Hispaniola; W&C CU, western and central Cuba; H, Hispaniola; ECU & NH, eastern Cuba and northern Hispaniola; PR, Puerto Rico; PR & CH, Puerto Rico and central Hispaniola; LA, Lesser Antilles.

element in *Nesiostrymon* subsequently vicariates as Cuba/Hispaniola + Puerto Rico.

If *T. hispaniola* is a southern Hispaniolan element [SH], further reference to Miller and Miller's models is necessary. Their five-step

Paleocene to Pliocene vicariance model (fig. 83) indicates the three-taxon statements of *Nesiostrymon* and *Terra* are congruent in this case *if* the Jamaica/southern Hispaniola distributions in both genera are viewed as them-
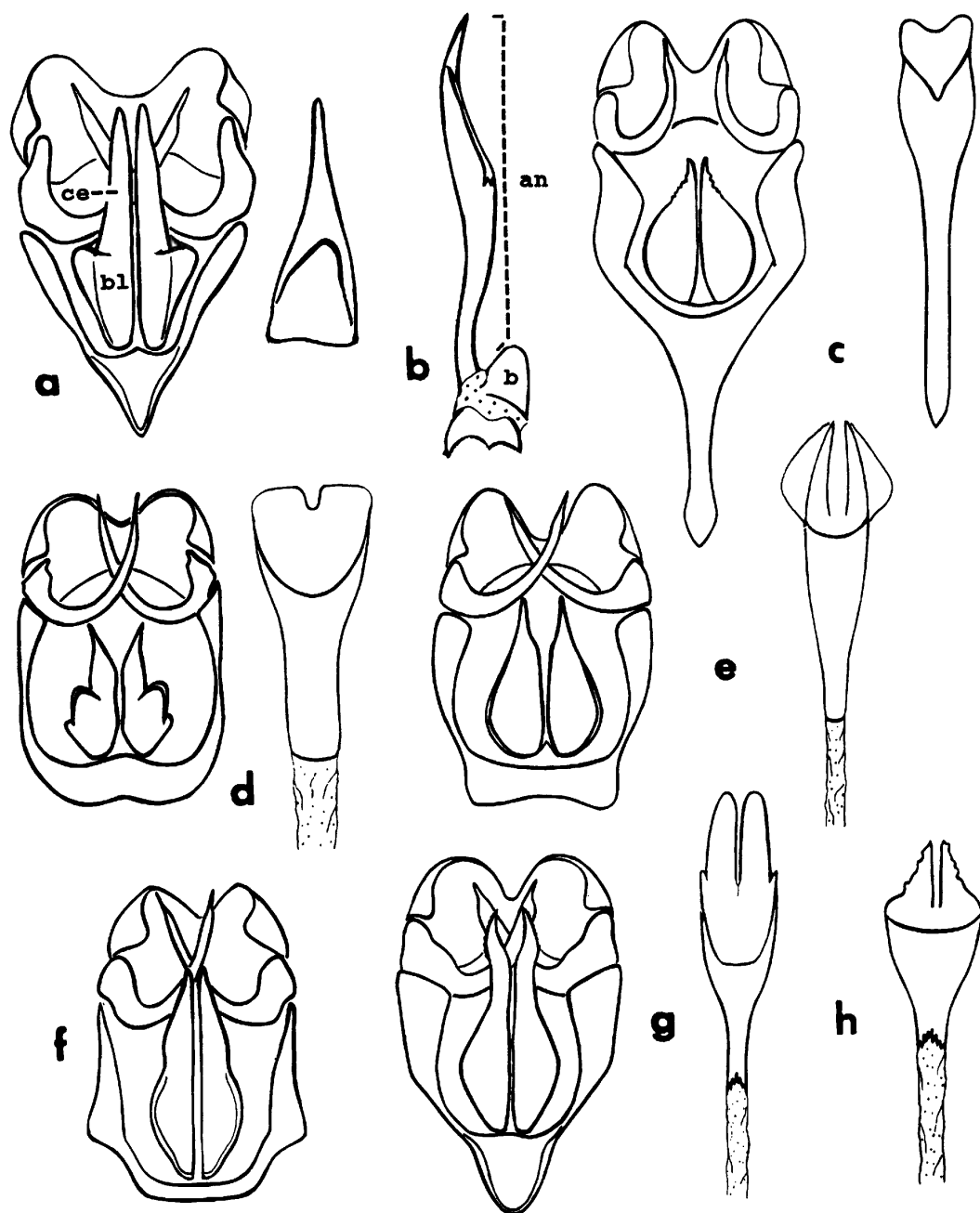
Fig. 84. Morphology of "*Thecla*" outgroups used in figure 1 cladogram construction (grouped according to Johnson and Matusik, 1988 [subsequent generic assignments by Johnson, 1991, in brackets]). All types BMNH and all views ventral, unless otherwise indicated. "*T. uzza* complex": **a.** *T. uzza* Hewitson [*Uzzia*], type male (left, male genitalia; right, male valvae, lateral view) showing lateral lobes considered precursor to *Nesiostrymon*; **b.** *Uzzia cotera* Johnson, holotype female, MNHN (genitalia, lateral view) showing condition primitive to female genital "bulb" of *Terra*. "*T. celmus* complex": group 1 [*Celmia*]; **c.** *Thecla celmus* Cramer (male left, female right), Presidio, Mexico, AMNH; group 2 [*Caerofethra*]; **d.** *T. seudiga* Hewitson (type male left, type female right, stipples here and in e, g, and h, illustrating membranous character of ductus bursae caudad of corpus bursae); **e.** *T. emandatus* Druce (type male left, type female right); **f.** *T. carnica* Hewitson, type male; **g.** *T. hesychia* Godman and Salvin (type male left, topotypical female right, Rio Sucio, Costa Rica, BMNH); **h.** *T. iambe* Godman and Salvin, type female. an, antrum; b, bulb; bl, bilobed configuration; ce, caudal extension.
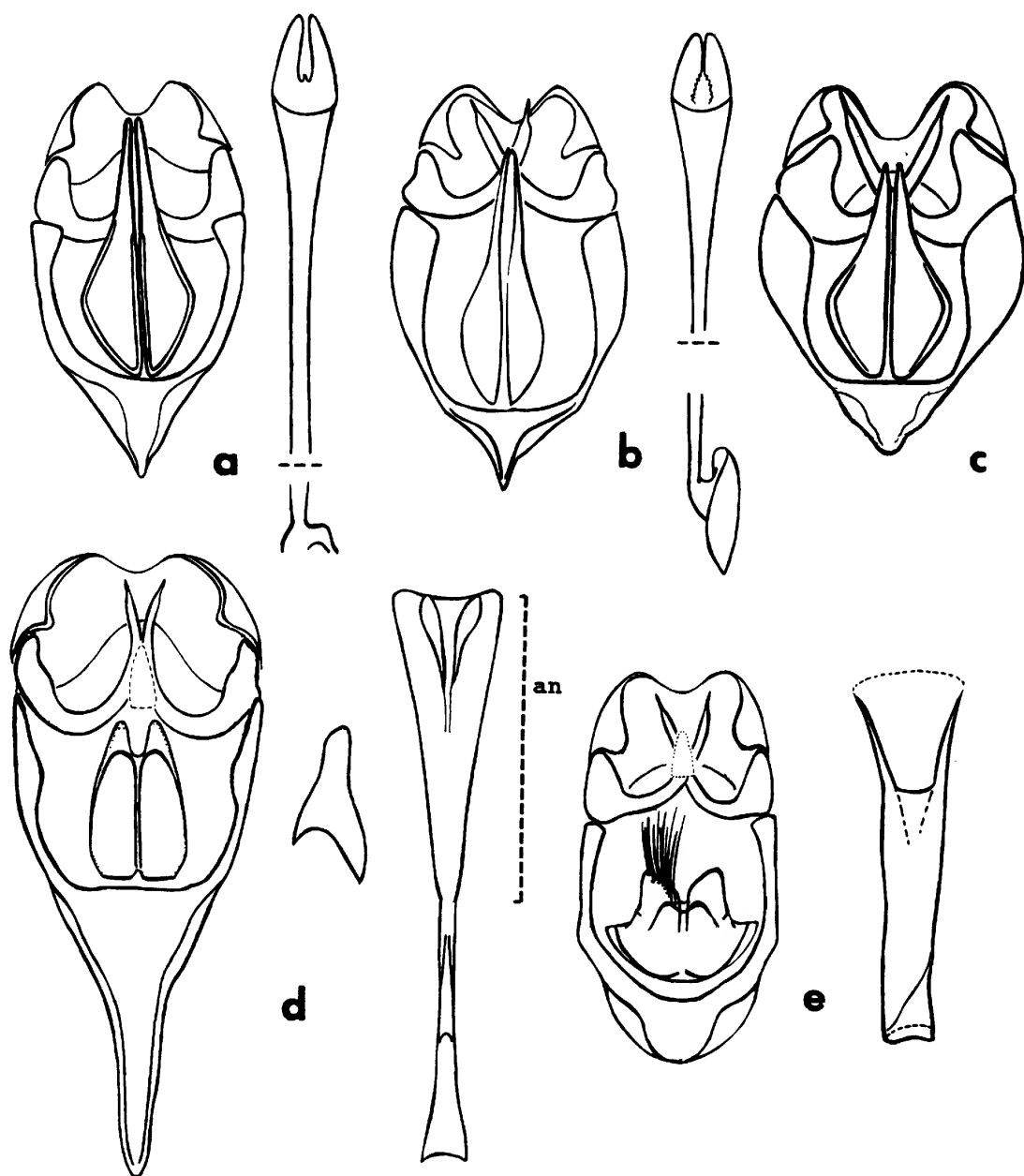
Fig. 85.   Morphology of "*Thecla*" outgroups used in figure 1 cladogram (grouped according to Johnson and Matusik, 1988 [subsequent generic assignments by Johnson, 1991, in brackets]). All types BMNH and all views ventral, unless otherwise indicated. "Outgroup complex" [*Aubergina*]: **a.** *T. alda* Hewitson (type male left, type female right, below dashed line, lateral view of cervix bursae); **b.** *T. paetus* Godman and Salvin (type male left, type female right, below dash line, lateral view of cervix bursae); **c.** *T. hicetas* Godman and Salvin, type male. Additional outgroup taxa of present study: group 1 [*Sipaea*]; **d.** *T. hyccara* Hewitson (type male left, female right, "Amazon," BMNH, showing conditions primitive to *Nesiostrymon/Terra*); group 2 (*Dicya*); **e.** *T. dicaea* Hewitson (type male left, showing condition primitive to *Nesiostrymon/Terra*, female right, Rio de Janeiro, Brazil, MPM). an, antrum.

selves representing the old Central American component of the ancestral distribution. With this assumption, the area cladograms are J/PGA + SA,CA; PGA/SA + CA for *Nesiostrymon* and SH [= cusp of PGA, Paleocene-Eocene]/SA + CA for *Terra.*

The ancestral distribution for proto-*Nesiostrymon/Terra* has been assumed here as proto-Greater Antilles, South America, and lower Central America, compatible with the Paleocene. It is important to point out that both *Nesiostrymon* and *Terra* have modern southern Mexican, Central American, and northern South American components (*N. celona, T. tera*) which are apotypic relative to Antillean congeners. In accord with the interpretation that *N. shoumatoffi* and *T. hispaniola* represent remnants of the ancestral Central American distribution of these genera, it is inferred that contemporary distributions of *N. celona* and *T. tera* reflect dispersion across the Pliocene–post-Pliocene reconnection of Central America and South America, as is typical of many other groups of organisms (Cruz, 1974; Bond, 1978; Olson, 1978; Savage, 1982). If widespread extinction has not been a historical factor, it appears that *Terra* is relatively younger than *Nesiostrymon,* since the former lacks a large proto-Greater Antilles component and the sole Antillean member is of limited distribution.

A dispersal model for *Nesiostrymon/Terra* is complex. The least complex view requires no fewer than two simultaneous and three sequential coincidental dispersals. Initially, an element of *Nesiostrymon* (*N. shoumatoffi*) must disperse solely to Jamaica while another element (*N. celida* complex) independently reaches Cuba, Hispaniola, and Puerto Rico in precisely the sequence of the Oligocene–early Miocene Antillean breakup. Simultaneously, an element of the sister genus *Terra* (*T. hispaniola*) must disperse solely to southern Hispaniola in a fashion allowing it to co-exist with *N. celida* populations in isolated upland mesic forest biomes. Even if one speculates that mesic forests were formerly more cosmopolitan in the Antilles, such dispersals appear exceedingly unlikely.

Considering the high consistency value in cladistic characters of *Nesiostrymon* and *Terra* and the geographic occurrence of member species, a dispersal explanation for their Antillean origin is cumbersome. On the contrary, the same cladistic and distributional data do not contravene a view that *Nesiostrymon* and *Terra* arose through late Cretaceous-Tertiary vicariance of elements on the Caribbean tectonic plate.

ACKNOWLEDGMENTS

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